Fishery Bulletin

Vol. 69, No. 4 October 1992

MENTER, SUSAN, 801. Some problems in estimating population sizes from catch-at-age data ... 819

HAYLOR, WILLIAM H. Integrity of schools of skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean as determined from tagging data ... 831

CARTES, MARGARIDA, and KARIM ERZINI. Comparison of two length-frequency based methods for estimating growth and mortality parameters using simulated samples with varying recruitment patterns ... 846

LIN, SHING-HWAN, and NANCY A. WILLIAMS. Specifying a Gompertz form for influence of hatchery smolt releases on adult salmon production ... 858

BEACHAM, TERRY D., CLYDE B. MURRAY, and RUTH E. WITHLER. Age, morphology, developmental biology, and biochemical genetic variation of Yukon River fall chum salmon, *Oncorhynchus keta*, and comparisons with British Columbia populations ... 880

ZASLO, M. B., and P. A. LIVINGSTON. Food habits and daily ration of Greenland halibut, *Reinhardtius hippoglossoides*, in the eastern Bering Sea ... 895

CROSS, JEFFREY N. Aspects of the biology of two scyliorhinid sharks, *Apristurus brunneus* and *Parmaturus xaniurus*, from the upper continental slope off southern California ... 931

SHANKS, ALAN L. Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish ... 946

HOBSON, EDMUND S., and JAMES R. CHESS. Trophic relations of the blue rockfish, *Sebastes mystinus*, in a coastal upwelling system off northern California ... 959

GRIMES, CHURCHILL B., CHARLES E. IDELBERGER, KENNETH W. ABLE, and STEPHEN C. TURNER. The reproductive biology of tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, from the United States Mid-Atlantic Bight, and the effects of fishing on the breeding system ... 744

HARGREAVES, N. B. A field method for determining prey preferences of predators ... 765

FORD, RICHARD F., BRUCE F. PHILLIPS, and LINDSAY M. JOLL. Experimental manipulation of population density and its effects on growth and mortality of juvenile western rock lobsters, *Panulirus cygnus* George ... 772

RAGHUNATHAN, DHANA F., and DONALD E. BRYANT-RICH. A study on the behavior and survival of early juvenile American lobster, *Homarus americanus*, in three naturalistic substrates: eelgrass, mud, and rocks ... 795

(Contents of next issue)

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Fishery Bulletin

The Fishery Bulletin is the ongoing research, survey and technical series of investigations in fishery science, engineering, and economics. The subjects of the United States Fish Commission Bulletin (1881 to 1926) and the Bulletin of the Bureau of Fisheries (1904 to 1940) are continued in the Fishery Bulletin of the Fish and Wildlife Service (1941 to 1970). Publication was issued at irregular intervals through volume 48 (by the Government Printing Office, 1908). Beginning with volume 49 (1938) and continuing through volume 65 (in 1965), each separate appeared as a numbered bulletin. A new system began in 1966 with volume 66 in which papers are bound together in a single issue of the bulletin instead of being published individually. Beginning with volume 70, number 1, January 1972, the Fishery Bulletin became a periodical, issued quarterly (or 4 times a year). It is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402. It is also available free to libraries, research institutions, State and Federal agencies, and to individuals by placing a standing order for it with the Publications Unit, Northwest Fisheries Center, 2725 Montlake Blvd. E., Seattle, WA 98112. Individuals may also obtain single issues from the Publications Unit.

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The Fishery Bulletin (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112. Second-class postage is paid at Seattle, Wash., and at additional mailing offices. POSTMASTER: send address changes for subscriptions to Fishery Bulletin, Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402.

Although the contents have been carefully edited and may be regarded as reliable, accuracy cannot be guaranteed.

The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing this periodical has been approved by the Director of the Office of Management and Budget.

Fishery Bulletin

CONTENTS

Vol. 86, No. 4 October 1988

MENDELSSOHN, ROY. Some problems in estimating population sizes from catch-at-age data 617
BAYLIFF, WILLIAM H. Integrity of schools of skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean, as determined from tagging data 631
CASTRO, MARGARIDA, and KARIM ERZINI. Comparison of two length-frequency based packages for estimating growth and mortality parameters using simulated samples with varying recruitment patterns 645
LIN, BIING-HWAN, and NANCY A. WILLIAMS. Specifying a functional form for the influence of hatchery smolt release on adult salmon production 655
BEACHAM, TERRY D., CLYDE B. MURRAY, and RUTH E. WITHLER. Age, morphology, developmental biology, and biochemical genetic variation of Yukon River fall chum salmon, *Oncorhynchus keta*, and comparisons with British Columbia populations 663
YANG, M. S., and P. A. LIVINGSTON. Food habits and daily ration of Greenland halibut, *Reinhardtius hippoglossoides*, in the eastern Bering Sea 675
CROSS, JEFFREY N. Aspects of the biology of two scyliorhinid sharks, *Apristurus brunneus* and *Parmaturus xaniurus*, from the upper continental slope off southern California 691
SHANKS, ALAN L. Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish 703
HOBSON, EDMUND S., and JAMES R. CHESS. Trophic relations of the blue rockfish, *Sebastes mystinus*, in a coastal upwelling system off northern California 715
GRIMES, CHURCHILL B., CHARLES F. IDELBERGER, KENNETH W. ABLE, and STEPHEN C. TURNER. The reproductive biology of tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, from the United States Mid-Atlantic Bight, and the effects of fishing on the breeding system 745
HARGREAVES, N. B. A field method for determining prey preferences of predators... 763
FORD, RICHARD F., BRUCE F. PHILLIPS, and LINDSAY M. JOLL. Experimental manipulation of population density and its effects on growth and mortality of juvenile western rock lobsters, *Panulirus cygnus* George 773
BARSHAW, DIANA E., and DONALD R. BRYANT-RICH. A long-term study on the behavior and survival of early juvenile American lobster, *Homarus americanus*, in three naturalistic substrates: eelgrass, mud, and rocks 789

(Continued on next page)

Seattle, Washington

1988

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington DC 20402—Subscription price per year: $16.00 domestic and $20.00 foreign. Cost per single issue: $9.00 domestic and $11.25 foreign.

BLAYLOCK, ROBERT A. Distribution and abundance of the bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), in Virginia 797

Notes

SEKI, MICHAEL P., and MICHAEL W. CALLAHAN. The feeding habits of two deep slope snappers, *Pristipomoides zonatus* and *P. auricilla*, at Pathfinder Reef, Mariana Archipelago 807
DITTY, JAMES G., GLEN G. ZIESKE, and RICHARD F. SHAW. Seasonality and depth distribution of larval fishes in the northern Gulf of Mexico above latitude 26°00′N ... 811
ROGERS, CHRISTOPHER W., DONALD R. GUNDERSON, and DAVID A. ARMSTRONG. Utilization of a Washington estuary by juvenile English sole, *Parophrys vetulus* ... 823
SAFRIT, GLEN W., and FRANK J. SCHWARTZ. Length-weight relationships for gulf flounder, *Paralichthys albigutta*, from North Carolina 832
WIEBE, PETER H. Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: a correction 833
GRAVES, JOHN E., MARIE A. SIMOVICH, and KURT M. SCHAEFER. Electrophoretic identification of early juvenile yellowfin tuna, *Thunnus albacares* 835
CAHOON, LAWRENCE B., and CRAIG R. TRONZO. A comparison of demersal zooplankton collected at Alligator Reef, Florida, using emergence and reentry traps ... 838

Index 847
Notice 860

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SOME PROBLEMS IN ESTIMATING POPULATION SIZES FROM CATCH-AT-AGE DATA

ROY MENDELSSOHN[1]

ABSTRACT

A new method for estimating population sizes from catch-at-age data is given. The method treats the observed population sizes as missing data and uses a combination of the Kalman filter and the EM algorithm to derive maximum likelihood estimates of the parameters and minimum mean square error estimates of the population sizes. The algorithm does not assume that the observation errors and the errors in the population dynamics are uncorrelated with equal variances, which is a common assumption of existing techniques. A new parameterization for both recruitment and fishing mortality is given, based on smoothness priors. Recruitment (or fishing mortality) is estimated as a nonparametric function of time by calculating an "optimal" tradeoff between goodness-of-fit and smoothness of the function. The algorithm allows for multiple sources of observations (fishing, surveys, etc.) and allows for missing data in the observations, which can arise if the different sources of the observations occur on different time scales. An example suggests that the new algorithm may better capture variation that is important when using the population estimates to study the role of the environment (or other exogenous variables) on the population dynamics.

I can address the motivation of this paper by considering a slightly modified version of a model proposed by Collie and Sissenwine (1983). Assume that the underlying population dynamics satisfy

$$N(a+1, t+1) = [N(a,t) - C(a,t)]\,\tilde{m} + w(a,t)$$

$$a = 1, A \qquad (1)$$

where $N(a,t)$ is the number of fish age a at time t, $C(a,t)$ is the catch of age a fish at time t, $\tilde{m} = exp(-m)$ is the mortality rate and the vector $w(t) = (w(1,t), \ldots, w(A,t))^r$ is a sequence of independent, identically distributed normal random vectors with mean 0 and covariance matrix Q, and for any vector a, the notation a^r denotes the transpose of the vector. We assume that the initial population vector $N(0)$ is gaussian with a mean of μ and covariance Σ.

The population itself is not observed. Instead we observe that

$$n(a,t) = q(t)N(a,t) + v(a,t) \qquad (2)$$

where q is an unknown parameter and the vector $v(t) = (v(1,t), \ldots, v(A,t))^r$ is a sequence of independent, identically distributed normal random vectors with mean 0 and covariance matrix R. It is assumed that $E(v(t)\ w(t)^r) = 0$; that is, the observation error and the underlying randomness in the population are uncorrelated. There is some interest in the value of the estimates of the $q(t)$ (or if mortality is to be estimated, in the estimate of $\tilde{m}$) but the major interest lies in estimating the unobserved population sizes $N(a,t)$. The estimates of the $N(a,t)$ should reflect not only the trend in the population, much as a regression might, but also the period-to-period variation of the population, such as might be related to environmental changes. This will be the emphasis throughout the paper.

The model described in Equations (1) and (2) differs from that of Collie and Sissenwine (1983) in that I do not assume that the mortality rate is known; here I allow the underlying population dynamics to be random, and the observation errors in Equation (2) to be additive rather than multiplicative. For known $\tilde{m}$, Collie and Sissenwine (1983) suggested minimizing

$$\sum_{t=1}^{T} \sum_{a=1}^{A} (v(a,t)^2 + w(a,t)^2) \qquad (3)$$

over the parameters (in our notation) $\theta = (q, N(t))$

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Manuscript accepted July 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

where $N(t)$ is the vector of unobserved population sizes. The concern here is not whether the multiplicative or additive form of the model is more correct, but rather what elements of the model are data, what are parameters, and how to calculate appropriate estimates of each.

If there were all-seeing observers, both the population process $N(t)$ and the observation process $n(t)$ would be available as data. Equations (1) and (2) imply a sequence of conditional probability distributions $f_N(N(t+1) \mid N(t), \theta_1)$ and $f_n(n(t) \mid N(t), \theta_2)$, where θ_1, θ_2 are parameters of the distributions to be estimated. Assuming additive gaussian errors, then θ_1 would include the mean vector $FN(t)$ and a covariance matrix that can be calculated recursively (see below). The mortality rate $\bar{m}$ serves as a constraint on the form of the estimates of the mean vector, much as in the theory of regression. Similarly, the parameters for the observation process are a mean vector $H(t)N(t)$ and a covariance matrix, where $H(t)$ in this case depends on the parameters $q(t)$ that constrain the estimates of the mean vector. With an all-seeing observer, both $n(t)$ and $N(t)$ are realized values of random vectors and hence, are the data to be used to estimate the unknown parameters of the distributions, θ_1 and θ_2.

Thus, the unobserved population sizes are most appropriately treated as missing data. The estimation scheme proposed by Collie and Sissenwine (1983) treats the $N(t)$ as parameters to be estimated. Little and Rubin (1983, 1987: sec. 5.4) showed that treating missing data as parameters in likelihood equations does not produce maximum likelihood estimates of the parameters unless the proportion of missing data approaches zero as the sample size increases. This is because much of the asymptotic theory of maximum likelihood estimation depends on the number of observations becoming large, relative to the number of parameters. Little and Rubin (1983, 1987) showed that for a regression-like situation, the bias due to treating data as parameters can be quite large.

The alternate approach discussed by Little and Rubin (1983, 1987) is to integrate out the missing data from the complete data likelihood and maximize this function over the parameters as usually defined in estimation theory. This is the approach taken by Shumway and Stoffer (1982a), who used the EM (expectation-maximization) algorithm of Dempster et al. (1977) and Kalman filtering to derive maximum likelihood estimates for the parameters of the model and minimum mean square error estimates of the missing data.

I can explain some of the problems with estimating Equations (1) and (2), using the likelihood of Equation (3). Under the gaussian assumptions of the model, the complete data log-likelihood is given by (Shumway and Stoffer 1982a)

$$-\frac{1}{2}\log|\Sigma| - \frac{1}{2}(N(0) - \mu(0))' \Sigma^{-1} (N(0) - \mu(0)$$

$$-\frac{T}{2}\log|Q| - \frac{1}{2}\sum_{t=1}^{T}(N(t) - FN(t-1))' Q^{-1}(N(t) - FN(t-1))$$

$$-\frac{T}{2}\log|R| - \frac{1}{2}\sum_{t=1}^{T}(n(t) - H(t)N(t))' R^{-1}(n(t) - H(t)N(t)) \quad (4)$$

where $F = \bar{m}I$ and $H(t) = q(t)I$. Similarly, the complete data log-likelihood in Equation (3) by substitution is

$$-\sum_{t=1}^{T} ||N(t) - FN(t-1)||^2 + ||n(t) - H(t)N(t)||^2. \quad (5)$$

Collie and Sissenwine (1983) noted that their estimation scheme assumes that the process and observation errors have the same variance. However, from Equations (4) and (5) it can be seen that they make the stronger and unlikely assumption that both the errors in the population dynamics and the errors in the observation process are uncorrelated. Further, we can see from Equation (4) that when the $N(t)$ are treated as parameters, the estimates of the $N(t)$ depend on the observed data $n(t)$ for $t = 1,T$. Following Shumway and Stoffer (1982a), the expected log-likelihood conditioned on the observed data comprises three parts: a term due to estimating the expected value of the initial population size,

$$-\frac{1}{2}\log|\Sigma| - \frac{1}{2}tr\{\Sigma^{-1}[P(0|T) + (N(0) - \mu) \times (N(0) - \mu)^T]\}, \quad (6)$$

a term due to the unobserved dynamics,

$$-\frac{1}{2}\sum_{t=1}^{T}\log|Q(t)| - \frac{1}{2}\sum_{t=1}^{T}tr\{Q(t)^{-1}[(N(t|T) - FN(t-1|T)) \times (N(t|T) - FN(t|T)^T + P(t|T) + FP(t-1|T)F^T - P(t-1|T) \times F^T - FP(t,t-1|T)]\}, \quad (7)$$

and a term due to the observation process,

$$-\frac{1}{2}\sum_{t=1}^{T}\log|R(t)| - \frac{1}{2}\sum_{t=1}^{T}tr\{R(t)^{-1}[(n(t) - H(t)N(t|T)) \times (n(t) - H(t)N(t|T))^T + H(t)P(t|T)H(t)]\} \quad (8)$$

where $N(t|s)$ denotes

$$N(t|s) = E[N(t) \mid n(1), \ldots, n(s)], \quad (9)$$

$P(t|s)$ denotes

$$P(t|s) = E[(N(t) - N(t|s)) \times (N(t) - N(t|s))^T \mid n(1), \ldots, n(s)], \quad (10)$$

and $P(t,t-1|s)$ denotes

$$P(t,t-1|s) = E[(N(t) - N(t|s)) \times (N(t-1) - N(t-1|s))^T \times \mid n(1), \ldots, n(s)]. \quad (11)$$

As shown in Equations (6) through (8), the proper estimates of the $N(t)$ and the related covariance matrices should be conditional expectations based on all of the data rather than on only the data up to time t. Assuming that all quantities are calculated properly, estimates that include only the data up to time $t-1$ are termed "predicted" estimates, estimates that include only the data up to time t are termed "filtered" estimates, while estimates given all the data are termed "smoothed" estimates. I shall show below that the appropriate formulas for predicted, filtered and smoothed estimates differ significantly. Thus using Equation (5) as the likelihood and treating the $N(t)$ as parameters does not produce proper estimates of the $N(t)$.

In the rest of this paper, I review state-space models and methods for estimating both the parameters and the unobserved components of the model. A very readable background for what follows is chapter 3 in Shumway (1988). The estimation scheme described does not require that the components of R, Q, and Σ have equal variance and are uncorrelated. Explicit estimates of these matrices are given. Then I show that a variety of age-based models proposed in the literature can be formulated as a state-space model, but that the formulations as presented make the same error of treating the unobserved components as parameters, and assume zero covariance in the errors. Auxiliary information as in Deriso et al. (1985) can be put into this format. And I show that the state-space formulation can include multiple observations of the population, but where some of the observations are missing. This can arise when the population is observed from fishing and from a variety of surveys, but some of the surveys are not done every year. This is essentially the problem discussed in Methot[2]. I give true maximum likelihood estimates for this model, allowing the different observation processes to have different error structures and estimate the relative weight that should be given each. This is a significant advance over the procedure in Methot (fn. 2).

A related paper is the analysis of Brillinger et al. (1980) who use a modified Kalman filter and maximum likelihood estimation to estimate the average birth and death rates and population structure of Nicholson's blow-fly data when only total numbers

[2]Methot, R. 1986. Synthetic estimates of historical abundance and mortality for northern anchovy, *Engraulis mordax*. Adm. Rep. LJ-86-29. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

of births and deaths at any time are available. In their model, knowing the births is equivalent to knowing the recruitment at each time period and the deaths are observed directly without error. Also, they appear to use the filtered estimates of the population structure, while the smoothed estimates are the minimum mean squared estimates given all the data. P. Sullivan[3] in his Ph.D. dissertation independently developed a length-based fishery model using Kalman filtering and maximum likelihood estimation.

I reiterate that the models considered here assume additive errors, while much of the existing literature prefers multiplicative errors, particularly for the observation equation. The basis of this preference appears to be that models with multiplicative errors have given a better "fit" to the data for other estimation schemes. In these estimation schemes the errors are assumed to have equal variances and are assumed to be uncorrelated. The better fit found for multiplicative errors in these algorithms may be due to these assumptions on the error variances. In effect, the errors are being scaled by the observed data which suggests that the assumption of equal variances is incorrect. In the present formulation I assume additive errors, but I can allow for errors with unequal variances, for errors that depend on the size of either the observed catch $n(a,t)$ or on the unobserved population $N(a,t)$, and for missing observations, and I can obtain simple to compute standard errors of the estimated underlying population sizes. The algorithm is also simple to program. If multiplicative errors are assumed, it is more difficult to calculate exact maximum likelihood estimates. Approximate likelihood methods (such as the extended Kalman filter) have known undesirable properties. When the full richness of the assumptions allowed in additive error models is used, it is an open question if multiplicative errors are to be preferred.

STATE SPACE MODELS

The State-Space Model can be written in the form (Jazwinski 1970; Anderson and Moore 1979; Ljung and Soderstrom 1983):

$$x(t) = F(t)x(t-1) + B(t)u(t-1) + Gw(t) \quad (12)$$

$$y(t) = H(t)x(t) + v(t) \quad (13)$$

where $x(t) = (x_1(t), \ldots, x_p(t))^T$ is the p-dimensional unobserved state of the system; $u(t) = (u_1(t), \ldots, u_p(t))^T$ is a p-dimensional vector of deterministic inputs; $y(t) = (y_1(t), \ldots, y_q(t))^T$ is the observed data of the system; $w(t) = (w_1(t), \ldots, w_p(t))^T$ is a sequence of zero mean normal vectors with common covariance matrix Q; $v(t) = (v_1(t), \ldots, v_q(t))^T$ is a sequence of zero mean normal vectors with common covariance matrix R; and F, B, G, and H are appropriately dimensioned matrices that may depend on an unknown parameter vector θ. Note that q, the dimension of the observation vector, can be larger than p, the dimension of the state vector. Thus several different observation processes of the underlying dynamics are allowed.

Using the same notation as in Equations (9) and (10), the predicted, filtered, and smoothed estimates of the state vector and the covariance matrices can be calculated recursively as follows: for prediction and filtering,

$$x(t|t-1) = F(t)x(t-1|t-1) + Bu(t-1) \quad (14)$$

$$P(t|t-1) = F(t)P(t-1|t-1)F(t)^T + GQ(t)G^T \quad (15)$$

$$K(t) = P(t|t-1)H(t)^T \times (H(t)P(t|t-1)H(t)^T + R(t))^{-1} \quad (16)$$

$$x(t|t) = x(t|t-1) + K(t) \times (y(t) - H(t)x(t|t-1)) \quad (17)$$

$$P(t|t) = P(t|t-1) - K(t)H(t)P(t|t-1) \quad (18)$$

where $x(0|0) = \mu$ and $P(0|0) = \Sigma$, and for smoothing,

$$J(t-1) = P(t-1|t-1)H(t)^T(P(t|t-1))^{-1} \quad (19)$$

$$x(t-1|T) = x(t-1|t-1) + J(t-1) \times (x(t|T) - x(t|t-1)) \quad (20)$$

$$P(t-1|T) = P(t-1|t-1) + J(t-1) \times (P(t|T) - P(t|t-1))J(t-1)^T. \quad (21)$$

The predicted state variable $x(t|t-1)$ differs from the quantity often used as the predicted value in the fisheries literature in that it is based on the last period's filtered estimate rather than on the last

[3]P. Sullivan, Center of Quantitative Sciences, University of Washington, Seattle, WA 98195, pers. commun. 1988.

period's predicted estimate. (For example, Deriso et al. (1985) suggested using backward VPA or cohort analysis to obtain predicted values.) The filtered estimate $x(t|t)$ is a weighted average of the predicted value of $x(t|t-1)$ and the observed error in estimating $y(t)$, where the weighting term $K(t)$ (the Kalman gain matrix) is regression-like. Similarly, the covariance of the estimate, as measured by $P(t|t-1)$, increases due to the prediction, but decreases by the amount $K(t)H(t)P(t|t-1)$ after the observation has been made. The smoothed estimate $x(t|T)$, which is the correct estimate of the underlying population (it satisfies the conditional expectation), is found by a backward recursion on the filtered estimates, where the filtered estimate is adjusted by a regression on the error between the smoothed and predicted estimates of the following period. Thus the smoothed estimates correct the predicted estimates both by the error in predicting the observed data as well as by the error in predicting the underlying population when using the filtered estimates of the underlying population. The square roots of the diagonal terms of the various P matrices produced by the Kalman recursions are the standard errors of the predicted, filtered, and smoothed estimates of the population.

Equations (12) and (13) are the basic form of the state-space model. It is a simple extension to the model to allow any of the matrices F, B, G, or H to be nonlinear functions of the past values of the $y(t)$ (see, for example, Shiryayev (1984), section VI.7), to allow the error vectors $w(t)$ and $v(t)$ to depend on past values of the $y(t)$ (Shiryayev 1984), or to allow the $v(t)$ to depend on the underlying state vector $x(t)$ (Zehnwirth 1988).

In a typical fisheries problem, the matrix $H(t)$ represents fishing. If some age-specific measure of effort $E(a,t)$ is known, then $H(t)$ is a diagonal matrix with $E(a,t)$ on the diagonals. Or it may be assumed that the exploitation rate is of the form $s(a)E(t)$, where $E(t)$ is known and the $s(a)$ values are to be estimated. Then for given values of $s(a)$, the matrix $H(t)$ has $s(a)E(t)$ on its diagonals. The matrix $F(t)$ is formed in a similar manner to represent the population dynamics.

In some parameterizations, it is assumed that a known vector is subtracted from the state vector either before or after the effect of F on the population. For example, the known vector might be the catch from the previous time period. The extension to the Kalman filter in this case is straightforward, an example of which can be found in Jazwinski (1970). Essentially, all predicted estimates of the state are corrected by the constant amount. The covariance and gain calculations are unaffected by the known vector.

The Kalman filter, Equations (14) through (21), assumes that the matrices F, B, G, H, R, Q, and Σ, and the vector μ are known. For fisheries problems, the matrices F and H usually depend on a set of parameters to be estimated (e.g., $F = mI$), and R, Q, and μ are to be estimated. Let θ be a vector containing the parameters that F and H depend on, and let $\Theta = (\theta, R, Q, \mu)$ be the total parameters of the model. Shumway and Stoffer (1982a) showed that conditional on Θ, the complete data likelihood is given by Equation (4). They apply a result of Dempster et al. (1977), which shows that maximum likelihood estimates of the parameters can be obtained by finding the conditional expectation (the E-step) of the complete data likelihood with respect to the missing "data" (in this case the missing data are the sufficient statistics of the normal distribution) and alternately estimating the expected value of the missing data, and then maximing the likelihood (the M-step) using the completed data. Shumway and Stoffer (1982a) showed that the expected conditional log-likelihood is given by Equations (6) through (8). All of the terms in this likelihood, for a given value of Θ, can be found by the Kalman filter. Moreover, given these values, the maximization problem is a deterministic one.

If we assume that the matrix F is independent of time and unrestricted, then Shumway and Stoffer (1982a) showed that the maximization step is accomplished by setting

$$F = S_t(1)S_{t-1}(0)^{-1} \tag{22}$$

$$Q = (S_t(0) - S_t(1)S_{t-1}^{-1}(0)S_t(1)^r)/T \tag{23}$$

$$R = T^{-1}\sum_{t=1}^{T}[(y(t) - H(t)x(t|T) \times (y(t) - H(t)x(t|T))^r + H(t)P(t|T)H(t)^r] \tag{24}$$

$$\mu = x(0|T). \tag{25}$$

where $$S_t(j) = \sum_{t=1}^{T}(P(t,t-j|T) + x(t|T)x(t-j|T)^r). \tag{26}$$

Shumway and Stoffer (1982a) gave a recursive formula for calculating $P(t, t-1|T)$ while performing the backward smoothing recursion.

If we assume that F is constrained to be of the form $F = \tilde{m}D$ where $\tilde{m}$ is a constant and D is a known matrix, then Shumway and Stoffer (1982b) showed that

$$Q = (C - \tilde{m}BD^{\tau} - \tilde{m}DB^{\tau} + \tilde{m}^2DAD^{\tau}) \quad (27)$$

$$\tilde{m} = \frac{tr(Q^{-1}BD^{\tau})}{tr(Q^{-1}DAD^{\tau})}. \quad (28)$$

Equations (27) and (28) can be solved by taking an initial guess for $\tilde{m}$, then iteratively solving for Q and $\tilde{m}$ until the values converge.

Finally, we can make explicit the effect of assuming equal variances and no covariances for both $w(t)$ and $v(t)$. For given estimates of Q and R, since both are square, symmetric matrices, they can be factored as

$$Q = U\,DU^{\tau}$$

$$R = LL^{\tau}$$

where U is an upper triangular matrix, D is a diagonal matrix, and L is the lower triangular square root of R. To obtain an underlying population dynamic that has an uncorrelated error vector $\tilde{w}(t)$ and uncorrelated observations with variances of 1, we make the following transformations:

$$\tilde{G} = GU$$

$$\tilde{y}(t) = L^{-1}y(t)$$

$$\tilde{H}(t) = L^{-1}H(t)$$

$$\tilde{v}(t) = L^{-1}v(t)$$

and replace G, w, y, H, and v in Equations (14) through (21) with the transformed values. Then $\tilde{v}(t)$ has covariance matrix I, and $\tilde{w}(t)$ has covariance matrix D. The assumption that both the error in the dynamics and in the observations are equal, further constrains the values of D to be identical. This is a very strong assumption.

AN EXAMPLE

As an example of these methods, I use the data for Pacific mackerel published in Parrish and MacCall (1978). I emphasize that I am only using these data for illustrative purposes and do not claim to be making a careful, thorough reexamination of the problem. Though $\tilde{m}$ can be estimated using Equation (28), I assume that the value of $\tilde{m}$ is known a priori. If I were to use a different value of $\tilde{m}$, it would be difficult to judge to what extent the new estimates differ solely due to the different mortality rate, rather than due to the estimation scheme. I assume, as in the reference, that the mortality rate m is equal to 0.5, so that the F matrix in my notation is a matrix with a value of 0.6065 in position $(i, i-1)$, $i = 2, \ldots, 7$, corresponding to the underlying dynamics for age groups 1 through 6.

Recruitment in Pacific mackerel is highly variable. I want to obtain estimates of recruitment that accurately reflect this variability while still being consistent with the observed data. Also, I do not want to a priori assume a functional relationship between recruitment and population size. To this end, I assume that the recruitment time series, after taking differences of a given order, is a random variable, i.e.,

$$\nabla^k r(t) = w(t) \quad (29)$$

where $w(t)$ is a normal random variable with a mean of zero and with an unknown variance σ^2 and ∇^k denotes kth order finite differencing. Akaike (1979) originally showed that this formulation is the discrete equivalent of fitting a spline to the data (in this case as a function of time), where the estimate of the variance σ^2 expresses the tradeoff between the degree of smoothness in the fitted curve with fidelity to the observed data. In this approach, k and the variance of $w(t)$ are treated as hyperparameters of the model. A fitting criterion such as AIC is then used to determine the best value of k given the data. Following Kitagawa and Gersch (1984), I could use smoothness priors to more generally decompose recruitment as

$$r(t) = T(t) + S(t) + \xi(t) + w(t) \quad (30)$$

where $T(t)$ is a trend term (as in Equation (29)), $S(t)$ is a seasonal term, and $\xi(t)$ is an irregular stationary term. A decomposition such as Equation (30) would be useful, for example, in modeling the monthly anchoveta recruitment considered in Mendelssohn and Mendo (1987). However, for convenience in this paper, I restrict recruitment to be of the form in Equation (29).

The relationship between this "smoothness priors" approach, "smoothing splines", and other penalized likelihood methods is discussed further for a variety of contexts in Brotherton and Gersch (1981), Kitagawa and Gersch (1984, 1985, 1988), Ansley and Kohn (1986), and Kohn and Ansley (1987, 1988). Wahba (1977) and O'Sullivan (1986) discussed the relationship between generalized cross-validation, penalized likelihood functions, and determining the tradeoff between smoothness and fit.

For $k = 0$, Equation (29) models recruitment as a random variable around a fixed but unknown mean value. For $k = 1$, Equation (29) models recruitment as a random walk with unknown mean level and drift (variance). Higher values of k have similar interpretations. Values of k higher than two or three rarely need to be considered, since these include the discrete equivalent of cubic splines. Cubic splines can approximate most functionals (in this case of time) to a reasonable degree of accuracy.

For this example, I assume $k = 1$, so that

$$r(t) = r(t - 1) + w(t) \tag{31}$$

which is a random walk with unknown variance. (A more complete analysis of this data would probably also include an irregular stationary term as in Equation (30) and determine the "best" order of differencing using a given criterion.) Equation (31) can be incorporated into the state space model by letting the (1,1) element of the matrix F be equal to 1. The matrices $H(t)$ are diagonal matrices whose values are calculated from table 13 in Parrish and MacCall (1978). Because I am assuming that the estimates of F are known, then the value of Q for the M step is maximized as

$$T^{-1}[S_t(0) - S_t(1)F^{\tau} - FS_t(1) + FS_{t-1}(0)F^{\tau}]. \tag{32}$$

As in Parrish and MacCall (1978), I treated age groups 4 through 6 as fully selected by the fishery, and will refer to these age groups as "adults". Similarly, I refer to the number of age-1 fish at the start of the season as the number of recruits. I assume that F and $H(t)$ are known, so the estimation problem is reduced to determining the means of the initial population sizes and the values of the two covariance matrices Q and R.

The resulting maximum likelihood estimates of Q and R (Tables 1, 2) show that the variances of the error terms differ by up to two orders of magnitude, hardly meeting the usual assumption of equal variances. Moreover, the covariances (expressed as correlations in the tables) are quite high, so that using $\frac{1}{\sigma}$ as a weighting factor will not be adequate. The predicted, filtered, and smoothed estimates of the adults (Fig. 1) are very similar, reflecting that the errors have been "filtered out" over time by the population dynamics.

TABLE 1.—Estimated values of the matrix Q presented as a variance-correlation matrix. The diagonal terms are the variances, and the off-diagonal terms are the cross-correlations.

	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
Age 0	8.72E+09	−0.9075	0.2429	0.0592	0.1785	−0.2096	0.0249
Age 1		4.59E+09	−0.1750	−0.0574	−0.1658	0.1803	−0.0432
Age 2			1.07E+09	0.0396	0.2416	0.1109	0.0675
Age 3				5.28E+08	0.7030	0.5964	0.3140
Age 4					1.90E+08	0.6717	0.3944
Age 5						3.08E+07	0.4854
Age 6							2.18E+06

TABLE 2.—Estimated values of the matrix R presented as a variance-correlation matrix.

	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
Age 0	7.30E+07	−0.0497	0.8505	0.7367	0.6594	0.5120	−0.4019
Age 1		2.62E+07	0.1594	0.0896	−0.0544	−0.3411	0.4325
Age 2			4.95E+06	0.6764	0.6412	0.3830	−0.2418
Age 3				3.43E+06	0.7286	0.4908	−0.2260
Age 4					7.11E+05	0.5708	−0.2030
Age 5						2.05E+05	−0.1331
Age 6							5.40E+04

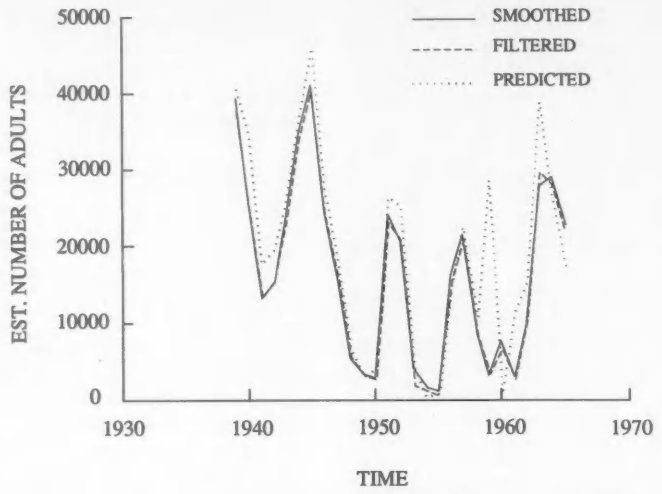

FIGURE 1.—Estimated number of adults, 1939–65, using values from Parrish and MacCall.

The predicted, filtered, and smoothed estimates of the recruits (Fig. 2), unlike those of the adults, are not similar. The filtered and smooth estimates are often indistinguishable, but there are some years (such as 1941 and 1943) where there are significant differences. The predicted values are very smooth, tending to emphasize the trend in the recruitment. In an analysis of recruitment estimates produced by standard cohort analysis of the anchoveta off Peru, Mendelssohn and Mendo (1987) found the estimates

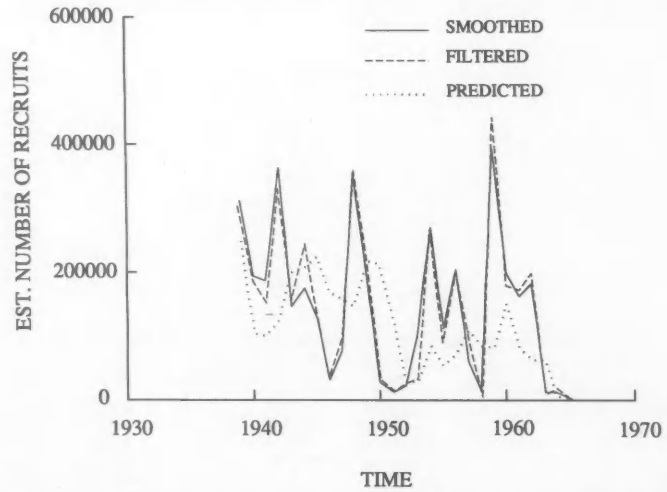

FIGURE 2.—Estimated number of recruits, 1939–65, using values from Parrish and MacCall.

to be far too smooth. The results of this present example may explain their observation. If these values were used in a subsequent analysis, say to determine the role of the environment on recruitment, a totally false picture of this relationship could emerge. I emphasize that the predicted estimates are calculated from the previous season's filtered values, whereas it is often true in the fisheries literature that the predicted values are estimated from the previous predicted values, rather than from the filtered values. Direct comparison with the estimate in Parrish and MacCall (1978) are difficult because restricting recruitment to be of the form (Equation (29)) with k fixed, rather than the more general form (Equation (30)) with k variable, may not be appropriate for the Pacific mackerel data. But overall, their estimates tend to resemble the smoother trend of my predicted estimates.

RELATIONSHIP TO OTHER LITERATURE AND A NEW PARAMETERIZATION

If the models are restricted to additive errors, then most of the simpler difference equation models proposed in Collie and Sissenwine (1983), Deriso et al. (1985), Fournier and Archibald (1982), Fournier and Doonan (1987), and among others can be formulated as I did. Some of these models assume recruitment is a nonlinear function of the underlying population, which cannot be handled in this model without some modifications (suggested below). However, all of these authors treat the underlying population sizes as parameters of the data rather than as missing data. As discussed earlier, it is questionable whether this will produce proper estimates of the underlying populations. Biases from treating missing data as parameters in a regression setting are explicitly discussed in Little and Rubin (1983, 1987).

A very broad class of possible models that can be selected to model catch-at-age data are given by Schnute (1985). He correctly identified the values that are parameters of the difference equations he discusses, and these are sufficient for estimating the likelihood (if evaluated properly). However, if we assume observation error, then it can be shown (see, for example, Shumway 1988) that the innovations are determined by predictors calculated from the previous period's filtered, rather than predicted values. Moreover, the minimum mean squared error estimates of the underlying populations, as discussed earlier, are the smoothed estimates. It appears that Schnute (1985) used the predicted or, at best, the filtered estimates of the underlying populations.

A popular parameterization that appears to have been first suggested by Doubleday (1976) is to assume that the observation matrix $H(t)$ is of the form $H(t) = \{s(a)f(t)\}$ where $s(a)$ is an age-dependent selectivity factor and $f(t)$ is a time-dependent exploitation rate. These values can be found by using a minimization routine during the M-step of the algorithm. However, it should be noted that the estimate of $f(t)$ for each t will depend on R and that the estimate of R will depend on both $s(\cdot)$ and $f(\cdot)$, so that either R, s, and f should be solved for together, or else they should be successively solved for using Equation (7) while holding the other parameter values fixed.

Alternatively, Equation (7) can be differentiated. Then for given values of $f(t)$, the optimum value of the vector $s(a)$ at each iteration are the diagonals of the matrix S given by

$$S = AB^{-1} \tag{33}$$

where $A = \sum_{t=1}^{T} y(t)x(t|T)^{\tau}f(t)$, and $B = \sum_{t=1}^{T} f^2(t)(P(t|T) + x(t|T)x(t|T)^{\tau}$. However, this is an unconstrained estimate and does not guarantee that $s(a)$ is between (0,1). It can be shown that the optimal solution is to set $s(a)$ at zero if $s(a)$ is negative or to 1 if $s(a)$ is greater than 1.

For fixed values of $s(a)$ and R, Equation (7) is maximized when $f(t)$ takes the value

$$f(t) = \frac{tr(R^{-1}y(t)x(t|T)^{\tau}S^{\tau})}{tr(R^{-1}S(P(t|T) + x(t|T)x(t|T)^{\tau})S^{\tau})} \tag{34}$$

where the matrix S is as above. This is the unconstrained solution. The constrained solution again is to force the estimate to lie within the closed interval $(0, 1)$ as with the estimate of the $s(a)$. Since the estimates of R, $s(a)$, and $f(t)$ are interrelated, I have found it to be a workable procedure to first estimate Q as given above and then for a given number of iterations, iteratively solve for $f(t)$ then $s(a)$. When these values stabilize, estimate R using the formula given above. While this procedure does not necessarily maximize Equation (7), it is sufficient for the generalized EM algorithm the new values increase the function given in Equation (7).

As with the original estimates, the smoothed and filtered estimates of recruitment (Fig. 3) are close

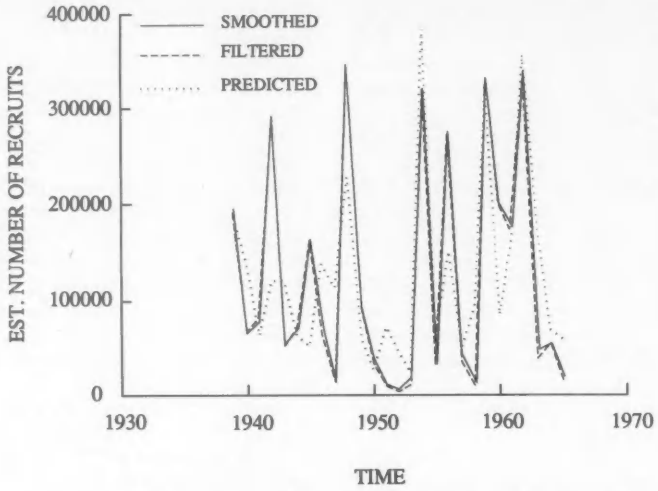

FIGURE 3.—Estimated number of recruits 1939–65, assuming $q(a, t) = f(t)s(a)$.

to each other, while the predicted values are too smooth. The estimated values of $f(t)$ (Fig. 4) generally decline with time. All three estimates are significantly different from the previous estimates. Years where relative highs and lows occur differ, showing the sensitivity of this class of models to the assumed form of the H matrix. Since the estimates of R, $s(a)$ and $f(t)$ are interrelated, I suspect that the parameter estimates are highly correlated and hence unstable. While I have not calculated the parameter covariance matrix, it should be checked for any serious analysis using these techniques.

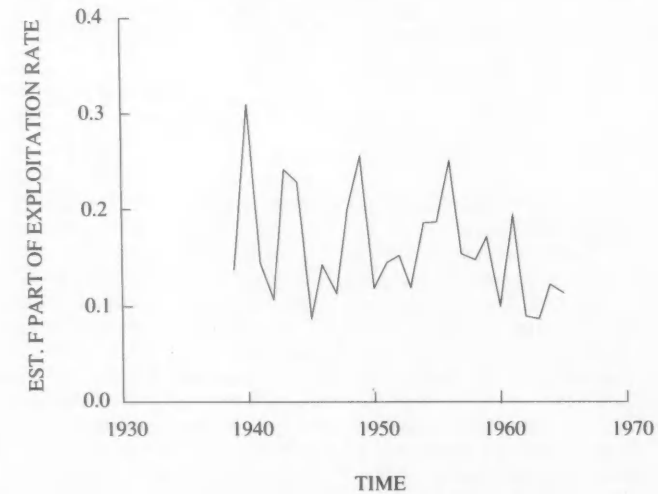

FIGURE 4.—Estimated values of $f(t)$ when $q(a, t) = f(t)s(a)$.

While the parameterization $H(t) = \{f(t)s(a)\}$ greatly reduces the number of parameters, I still face the same problem as when I treated the unobserved population as parameters: each new period adds another parameter to the model. The model still appears to be overparameterized, and the asymptotic theory for maximum likelihood estimation may be invalid.

As with the recruitment estimates, the number of effective parameters can be reduced by adding a smoothness prior on $f(t)$. However, $f(t)$ is a proportion and not likely to be a normal variable. The $f(t)$ are also constrained to lie in the interval $(0,1)$, so a transformation to an unconstrained variable would also be desirable. If $f(t)$ is a binomial random variable then $\arcsin(\sqrt{f(t)})$ is approximately normal with nearly equal variance. This suggests the transformation of variables

$$f(t) = \sin^2(e(t)) \tag{35}$$

where $e(t)$ is an unconstrained normal variable. Then the smoothness prior becomes

$$\nabla^k e(t) = w(t) \tag{36}$$

(a smoothness prior that includes a seasonal component or irregular stationary part, as in Equation (30), can also be used), and for any age class, the observation equation becomes

$$y(a,t) = s(a)\sin^2(e(t))x(a,t). \tag{37}$$

The underlying population dynamics must also be expanded to include the smoothness prior constraint (Equation (36)).

Unfortunately, the observation equation is no longer linear in the state vector. The smoothness prior is a prior distribution on the $f(t)$, and a full Bayesian analysis can be done to obtain the overall distribution. The variance of $w(t)$ is then treated as a hyperparameter in the analysis.

A simpler approach is to evaluate the filter equations approximately by using any one of a number of nonlinear filters (see Anderson and Moore 1979). One that is easy to implement, given the nonlinearities in this problem, is the extended Kalman filter (EKF), which at each time period just linearizes all the nonlinear terms around the value of the predicted state vector. The EKF, however, can have divergence problems and is not guaranteed to find the true penalized likelihood estimates.

When using the EKF, it works to make a forward and backward pass of the filter given the current estimates of $f(t)$ and $x(t|T)$, and then to estimate $s(a)$ and R as before. I tested the algorithm on the mackerel data with $k = 1$ in the constraint (Equation (36)). The resulting estimates (Fig. 5) are similar to the previous estimates, but the estimated values of $f(t)$ (Fig. 6) are less variable with a stronger trend than before. It is clear from Figure 5 that the

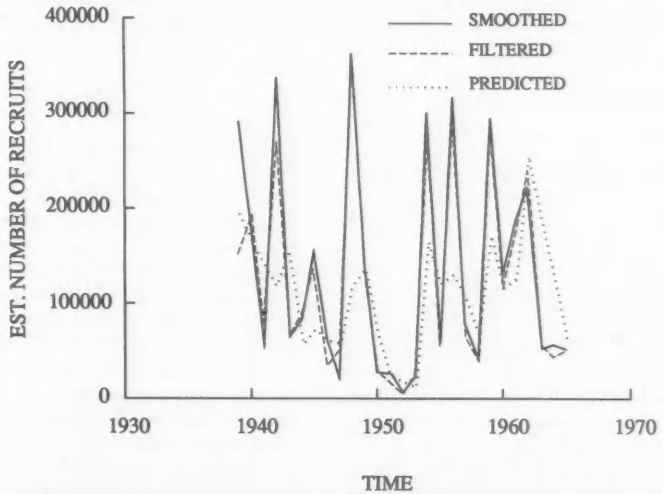

FIGURE 5.—Estimated number of recruits using a first order spline for estimating $f(t)$.

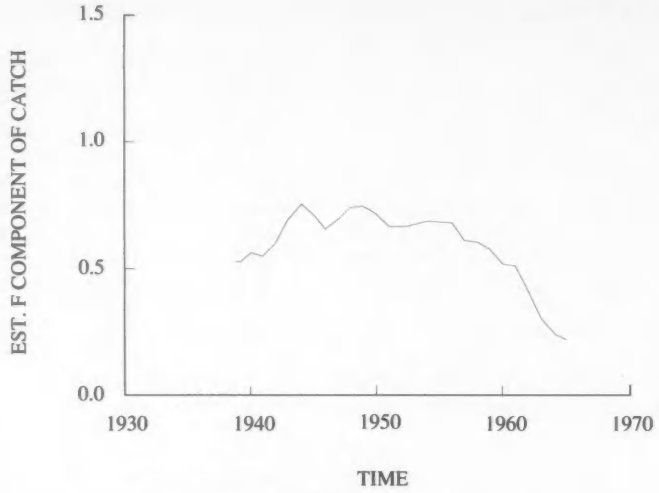

FIGURE 6.—Spline estimates of $f(t)$.

smoothness prior estimate has shifted some of the variation in the observed data to variations in the underlying population dynamics rather than variations in $f(t)$. Further research needs to be done to see which of these estimates is the most "valid".

The EM algorithm in general can be sensitive to the initial values given the parameters (see Wu 1983), and I have found that the fixed value of Σ can also affect the estimates. Initial combinations of μ, $f(t)$, and $s(a)$ that are totally inconsistent with the observed catch data can cause the algorithm to find a local maximum. This can be avoided by experimenting with several, very different starting values and determining if they converge to the same estimates.

If recruitment is thought to be a linear function of the previous population size, then there is no problem including this in the Kalman filter. If recruitment is a nonlinear function of the previous population, then the EKF can again be used to approximately determine the conditional expectations needed for the EM algorithm.

If information is available from a variety of sources, say from fishing and from surveys, as in Methot (fn. 2), then each of the vectors and matrices can be partitioned to represent this situation. For example, let $y_s(t)$ be the observed catches from a survey and $y_f(t)$ the observed catches from fishing. Let $y(t)^T = (y_s(t), y_f(t))^T$, and partition the H matrix similarly. Then the diagonal blocks of H will contain the observation dynamics for the survey and for fishing, while the off-diagonal blocks will be zero. Given these modifications, all the algorithms described previously in this paper can be used to derive estimates for this situation.

Research or other surveys of the fishery usually occur less frequently than does commercial fishing, causing part of the vector $y(t)$ to be missing at given times periods. Shumway and Stoffer (1982a) and Shumway (1988) gave a straightforward modification of the Kalman filter for this case.

DISCUSSION

I have introduced a new method for estimating population sizes from catch-at-age data that includes, if additive errors can be assumed, many of the previous difference equation models. I show that it is incorrect to treat the unobserved population sizes as parameters to be estimated rather than as missing data. I also show that the minimum mean square estimates of the population sizes are the smoothed estimates rather than the predicted estimates suggested in many papers. The model assumes neither equal variances in the errors in the population dynamics nor in the observation errors and does not require that the errors be uncorrelated. For Pacific mackerel, the smoothed estimates are shown to be much more variable than the predicted estimates.

I also suggest a new parameterization for the age-specific exploitation rate $q(a,t)$. If it is assumed that $q(a,t) = s(a)f(t)$, then the model is over determined. I put a smoothness prior on $f(t)$ in order to obtain a tradeoff between the degree of smoothness in $f(t)$ as a function of time versus fidelity to the data. The degree of differencing can be treated as a hyper-parameter of the model to determine the optimal amount of differencing given the data.

An advantage of the approach of this paper is that the calculations are straightforward and simple to program, and explicit formulas are given for the optimal parameter values at each iteration of the EM algorithm. Additional optimization software is not required to perform the calculations. Moreover, properties of the Kalman filter and the EM algorithm are well known. There is a large literature giving variants of the filter to calculate sensitivity to model misspecification, and recursive formulas for the derivatives with respect to a given parameter of the model also exist in the literature.

It is also simple to include environmental variables into the formulation, either as additional state variables or as fixed effects in the observation equation or both (see Sallas and Harville [1988] on how to estimate the fixed effect parameters within the context of Kalman filtering). Thus the influence of the environment can be modeled directly, rather than resorting to the conventional practice of obtaining population estimates first and correlating these estimates with the environmental variables second.

A disadvantage of my approach is that there is no guarantee that any of the estimates of the underlying population sizes will be positive. The population sizes are treated as normal random variables, and it is quite possible for the additive corrections in the filtered or smoothed estimates to make small population sizes negative if the observation error is large. P. Sullivan (fn. 3) has found that for a length-based model the Kalman filtering approach works best when there are pulses in the recruitment, that is, when the population is not in equilibrium. The likelihood surface is such that without recruitment pulses it is difficult to estimate the parameters of the growth-curve. Most fisheries are not in equilibrium, however. As the models in this paper do not contain a growth-curve, it is unclear if a similar finding will be valid.

Some of my results suggest that the estimates are sensitive to the form of the model chosen for the population dynamics. This is not surprising, because, unlike most missing data problems, the missing part of the data is never observed directly, but only through the presumed form of the dynamics. For example, when modeling catch (or catch per unit effort) against an environmental variable, catch data often are not available for all periods. But there are at least some periods when both variables are observed, which can be used to estimate the relationship between the two sets of variables. This relationship is used to produce the smoothed estimates of the missing data. For estimating population sizes from catch-at-age data, the a priori estimate of the form of the observation equation replaces this empirically derived estimate.

In many of the references cited, multiplicative errors are preferred in the observation equation because variances appear to change with the size of the population. My experience is that relaxing the assumption of equal, uncorrelated errors appears to at least partially take into account the observed differences. If the model estimates are not satisfactory, assuming additive, gaussian errors, then the regular EM algorithm can be used to properly estimate the smoothed estimates of the underlying population. However, the EM algorithm requires the complete data likelihood as well as the expectation of the log-likelihood with respect to $(y(1), \ldots, y(T))$. In multiplicative models, assumptions about the error structure can lead to very complicated multivariate distributions for the complete data due to the Jacobian of the transformation. The conditional expectation of the log-likelihood may have to be evaluated by numerically integrating a nontrivial multiple integral. Certainly, as a first pass, the simpler techniques of this paper would appear to have a lot to offer as an alternative.

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INTEGRITY OF SCHOOLS OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*, IN THE EASTERN PACIFIC OCEAN, AS DETERMINED FROM TAGGING DATA

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ABSTRACT

Little information concerning the integrity of schools is available for any species of fish. In this study the integrity of schools of skipjack tuna, *Katsuwonus pelamis*, was analyzed with data for returns of tagged fish which had been in the same schools when originally tagged. Two methods, the first using Chi-square contingency tests and the second using binomial homogeneity tests, were employed. From the results obtained with the first method it appears that after 1 month at liberty the tagged and untagged fish were randomly mixed with one another in some cases and after 3 to 5 months at liberty they were randomly mixed with one another in nearly all cases. The results obtained with the second method indicate somewhat less rapid mixing of the tagged and untagged fish.

Schooling occurs in many species of fish, and many studies have been made of the reasons for schooling and the behavior of the fish in the schools (e.g., Parr 1927; Shaw 1970; Pitcher 1986). Almost nothing has been written, however, about the integrity of schools over extended periods of time.

Parr (1927) stated that "apparently permanent" schools are formed by pelagic fishes such as mackerel, sprat, and herring, and Sharp (1978) reported that, "From the genetic sample data for the eastern Pacific yellowfin [(*Thunnus albacares*)] and the Pacific-wide skipjack [(*Katsuwonus pelamis*)] there is evidence for a cohesiveness of related fishes in schools.... What is observed is that where more than one very rare allele (overall expected occurrence <.01) is encountered in a large sample, the individuals exhibiting the rare alleles are often the same length or within 1 cm of each other. This is highly unlikely unless they are related."

On the other hand, Helfman (1981) reported "aggregations [of freshwater fish] that disbanded during twilight," and Moyle and Cech (1982) stated that "most schools break up at night." Observers on fishing vessels and aircraft have reported that the schools of tunas frequently break up and reform. Scott and Flittner (1972), for example, stated that "the relatively large nighttime schools [of bluefin tuna, *Thunnus thynnus*,] break down into several smaller foraging schools and begin their search for food.... The gradual increase in school size during the daylight hours may be due to regrouping of the smaller schools through random encounters." Such observations might lead to the conclusion that there is considerable mixing of fish from different schools and that fish of the same species and same approximate size in the same areas would mix thoroughly with one another within a period of a few days or weeks.

Anonymous (1960) stated that "Tag returns from individual schools [of skipjack tuna] suggest that, normally, the skipjack in Hawaiian waters remain within a school for one month or less, then at least some of the school break off, move into new areas, and regroup with other fish or schools. From the releases off Hilo and Mexico, however, it is evident that there are situations, possibly environmentally conditioned, where the schools remain intact...for at least 2 or 3 months." Lester et al. (1985) studied the occurrence of various parasites in skipjack tuna of the same and different schools and concluded that "school half-life is likely to be in terms of at least weeks rather than days." They stated, however, that their data did "not support the hypothesis [of Sharp (1978)] that fish stay in the same school for life."

Examination of data for fish tagged and released at the same location and time shows that some have been recaptured weeks or months later in the same purse seine set or baitboat stop, and others have been recaptured weeks or months later on the same date in widely separated locations (Hunter et al.

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Manuscript accepted July 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

1986). (Henceforth in this report, to save space, both sets and stops will be referred to as sets.) The former results might be due merely to chance. The latter results indicate that not all the fish remain together at all times, but this information is of limited value. A much more powerful method of analysis is needed. Turner (1986) employed statistical tests to show that tagged bluefin tuna caught during the calendar year after release had mixed considerably with the untagged population, but knowledge about shorter term mixing is necessary for short-lived species, such as skipjack tuna. The present report describes what are believed to be new and useful methods of analysis of the integrity of schools of fishes, using data for tagged skipjack tuna released and recaptured in the eastern Pacific Ocean.

MATERIALS AND METHODS

The methods of tagging the fish are described by Bayliff and Holland (1986).

Tagged fish, or tags unaccompanied by the fish to which they were attached, are recovered and returned by fishermen, unloaders, and cannery workers, accompanied by information which is used to assign them to specific sets. Additional details regarding this aspect of the study are discussed later in this report.

The methods of collecting and processing the catch statistics are discussed by Shimada and Schaefer (1956) and Joseph and Calkins (1969). Hennemuth (1957) and Shingu et al. (1974) described the methods of sampling the fish and the calculations employed to determine the size composition of tunas in the catches. The areas shown in Hennemuth's figure 1 have been changed several times since that report was published, however; the areas used currently are shown by Peterson (1982: fig. 30).

ANALYSES AND RESULTS

If tagged fish released at the same location on the same day mix thoroughly with the population of untagged fish in the same area, schools of fish caught in that area will have approximately equal ratios of tagged to total fish, whereas if they do not mix thoroughly some of the schools will have much higher ratios than the others. In this report the numbers of tagged fish recaptured in sets made at various intervals after release are compared with the numbers of tagged fish which would be expected in those sets if the tagged fish had mixed thoroughly with the rest of the population during the interval

TABLE 1.—Data used for analysis of integrity of schools of skipjack tuna. The ranges of values of sets and average weight in pounds are explained in the text.

Tagging cruise	Dates of release	Month of recapture	Numbers of returns	Sets	Average weight in pounds
1042	2, 3, 4, 17, 18, 19, 23, 24 June 1962	June	439	60–228	5.86–6.84
		July	152	174	5.85
		August	44	333	4.96
1043	5, 9, 20, 27, 28 June; 1 July 1963	June	130	11–89	6.10–6.27
		July	248	265–282	6.08–6.10
		August	108	385	5.74
		September	39	388	6.99
		October	13	247	4.98
1070	12, 13, 14, 30 June 1973	June	7	118–129	5.21–5.22
		July	32	144	5.08
		August	15	120	4.59
		September	27	45	5.35
		October	33	205	5.26
		November	10	229	5.69
1075	26 June; 20, 21 (two releases) July 1975	July	13	42–215	5.56–6.12
		August	55	274	6.83
1079	9, 10, 17, 18, 19 June 1976	June	158	232–297	4.31–4.32
		July	261	386	4.29
		August	15	47	4.24
		September	118	542	4.88
		October	61	546	4.56
		November	6	262	4.12

between release and recapture. A description of how this was done is given below. The data used in the analyses are summarized in Table 1, and a more detailed summary of the data for tagging cruise 1079, which will be discussed in more detail than the other cruises, is given in Table 2.

First, the units of time to be employed were selected. Tagged skipjack tuna have been recaptured after as long as 3 years at liberty, but the great majority of recaptures have been made within 6 months after release. It was decided to examine the data by monthly intervals because, for the experiments with sufficient total numbers of returns, that would produce several intervals with sufficient numbers of returns of tagged fish for each interval. Also, the statistical and size-frequency data of the Inter-American Tropical Tuna Commission (IATTC) are routinely calculated by month (and quarter and year), so no special calculations are required.

TABLE 2.—Data from cruise 1079 used for analysis of integrity of schools of skipjack tuna.

Date of release	Month of recapture	Numbers of returns	Sets	Average weight in pounds
9 June 1976	June	13	297	4.32
	July	13	386	4.29
	August	1	47	4.24
	September	5	542	4.88
	October	3	546	4.56
	November	0	262	4.12
10 June 1976	June	26	294	4.32
	July	17	386	4.29
	August	0	47	4.24
	September	8	542	4.88
	October	5	546	4.56
	November	1	262	4.12
17 June 1976	June	80	252	4.32
	July	120	386	4.29
	August	9	47	4.24
	September	48	542	4.88
	October	31	546	4.56
	November	1	262	4.12
18 June 1976	June	33	240	4.32
	July	88	386	4.29
	August	4	47	4.24
	September	43	542	4.88
	October	18	546	4.56
	November	2	262	4.12
19 June 1976	June	6	232	4.31
	July	23	386	4.29
	August	1	47	4.24
	September	14	542	4.88
	October	4	546	4.56
	November	2	262	4.12
Total	June	158	297	4.32
	July	261	386	4.29
	August	15	47	4.24
	September	118	542	4.88
	October	61	546	4.56
	November	6	262	4.12

Second, the areas of study were selected. If the tagged fish are released at a particular location, the vessels fishing near that location would catch more tagged fish, at least during the first few months after release, than would vessels fishing several hundred or more miles away. Thus only data for the vessels fishing near the location of release should be considered. The areas of study were selected by examining charts of the distributions of fishing effort and recaptures of tagged fish, by 1-degree areas and by months, and arbitrarily excluding those with lower recaptures per unit of fishing effort. This was quite simple, as during the periods in question practically no tagged fish were recaptured south of lat. 20°N, and there was little fishing effort north of lat. 20°N outside the area-time strata selected. The areas of study for the data for tagging cruise 1079 are shown in Figure 1.

Third, a list of sets for each area-time stratum was prepared. This included the weights of skipjack tuna caught (Table 3, column 2) and the numbers of tagged fish returned (Table 3, column 4). (Throughout this report the weights are expressed in short tons [0.907 metric tons] and pounds [0.454 kg]. The IATTC uses this system because the fishermen estimate the weights of the fish caught in individual sets in short tons, and these estimates are an important component of its data base.) In a few cases the catches were recorded only as weights of mixed skipjack tuna and some other species, and in those cases the weights were divided by 2, assuming that they consisted of equal weights of skipjack tuna and the other species. (The rest of this table will be discussed later.)

It can be seen in Table 1 that ranges instead of individual values are given for "Sets" for cases when the month of recapture is the same as the month of release. This is because sets made before the date of release were not considered for the analyses, and it was also decided not to use data for tagged fish recaptured on the date of release because these could not have mixed with the rest of the fish in the area to any appreciable extent. Therefore for cruise 1079, for example, there were 297 June sets after 9 June, 294 after 10 June, 252 after 17 June, 240 after 18 June, and 232 after 19 June (Table 2).

Fourth, an average weight for each month of recapture for each experiment was selected. Monthly average weight data for purse seine- and baitboat-caught fish from area 1 in Peterson (1982: fig. 30) were used for this purpose because they closely correspond to the strata selected for study. The aver-

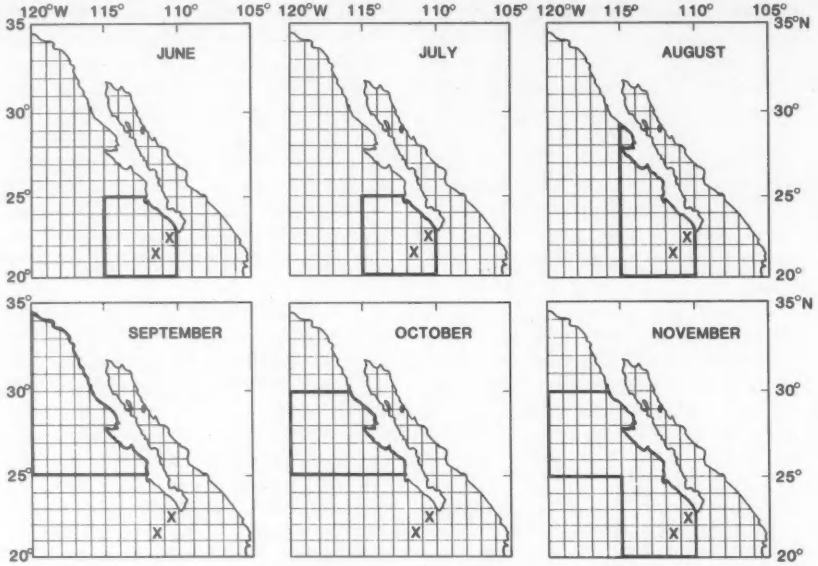

FIGURE 1.—Locations of release (X's) and areas of recapture selected for tagging cruise 1079 (areas delineated by heavy lines).

age weights were estimated by

$$\bar{w}_j = \frac{\left(\sum_{i=1}^{n} W_{ijPS} \times \bar{w}_{jPS}\right) + \left(\sum_{i=1}^{n} W_{ijBB} \times \bar{w}_{jBB}\right)}{\sum_{i=1}^{n} W_{ijPS} + \sum_{i=1}^{n} W_{ijBB}}$$

where $\bar{w}_j$ = average weight of skipjack tuna in stratum j,

W_{ijPS} and W_{ijBB} = weights of skipjack tuna caught in purse seine set i and baitboat set i, respectively, made in stratum j,

n = number of purse seine or baitboat sets in stratum j, and

$\bar{w}_{jPS}$ and $\bar{w}_{jBB}$ = average weights of skipjack tuna caught in stratum j by purse seiners and baitboats, respectively.

These are listed in Tables 1 and 2.

The average weights usually differ within strata which correspond to the months of release (Tables 1, 2) because only the sets after the dates of release are considered, and the portions of the total catches which are from purse seines and baitboats differ in accordance with the dates considered.

The data were analyzed by 1) Chi-square contingency tests and 2) the binomial homogeneity test described by Kendall and Stuart (1961:578–579).

Chi-Square Contingency Tests

A computer program, SCHOOL, was written to analyze the data. For a given release date and month of recapture, this program estimates the number of fish caught in each set from the weight of fish caught and the average weight of the fish. It then sums the estimates of the numbers of fish caught and numbers of tagged fish returned for all sets and calculates the tagged to total ratio. This ratio is then used with the equation for the binomial distribution to estimate the probabilities of 0, 1, 2, 3,. . . tagged fish appearing in each set if the fish are randomly mixed. The sums of the probabilities for all the sets for 0, 1, 2, 3,. . . tagged fish are then calculated so that these can be compared with the observed data, as described in the next paragraph. A sample output

from this program is shown in Table 3. It can be seen that the sum of 39.40 + 6.41 + 1.00 + 0.16 + 0.02 (last line) is equal to 47, the number of sets, and that the sum of (39.40 × 0) + (6.41 × 1) + (1.00 × 2) + (0.16 × 3) is equal to 9, the number of tagged fish returned. (The numbers of tagged fish returned for each set had been entered in Table 3, column 4, as explained above. If the total, 9, had been entered for the first set, or any other set, however, the result in the bottom line would have been the same.)

The bottom lines from all the outputs from SCHOOL for tagging cruise 1079 are listed in the "exp." (expected) lines of Table 4. Just below these are listed the observed ("obs.") numbers of sets with 0, 1, 2, 3, . . . tagged fish. At the bottom of each section of this table the sums of the expected and observed values are listed. Chi-square tests were run, using MINITAB (Ryan et al. 1985), on the expected

TABLE 3.—Probabilities of 0, 1, 2, 3, . . . 10 tagged fish in sets made in August in the area shown in Figure 1 from fish released on 17 June 1976. This table is similar to the output from program SCHOOL except that (1) normally the lines for the individual sets are not printed and (2) the output does not include the numbers of fish.

			Tags											
Set	Tons	Fish		*P*(0)	*P*(1)	*P*(2)	*P*(3)	*P*(4)	*P*(5)	*P*(6)	*P*(7)	*P*(8)	*P*(9)	*P*(10)	Total
1	12.0	5,660	0	0.6921	0.2546	0.0468	0.0057	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
2	15.5	7,311	1	0.6217	0.2954	0.0702	0.0111	0.0013	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
3	15.0	7,075	0	0.6313	0.2903	0.0667	0.0102	0.0012	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
4	5.0	2,358	0	0.8578	0.1314	0.0101	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
5	3.0	1,415	0	0.9121	0.0838	0.0038	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
6	1.0	472	1	0.9698	0.0296	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
7	2.0	943	0	0.9405	0.0575	0.0018	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
8	1.0	472	0	0.9698	0.0296	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
9	25.0	11,792	0	0.4646	0.3561	0.1365	0.0349	0.0067	0.0010	0.0001	0.0000	0.0000	0.0000	0.0000	0.9998
10	25.0	11,792	0	0.4646	0.3561	0.1365	0.0349	0.0067	0.0010	0.0001	0.0000	0.0000	0.0000	0.0000	0.9998
11	1.0	472	0	0.9698	0.0296	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
12	1.0	472	3	0.9698	0.0296	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
13	1.0	472	0	0.9698	0.0296	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
14	2.0	943	0	0.9405	0.0575	0.0018	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
15	5.0	2,358	0	0.8578	0.1314	0.0101	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
16	5.0	2,358	0	0.8578	0.1314	0.0101	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
17	9.0	4,245	0	0.7588	0.2093	0.0289	0.0027	0.0002	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
18	5.0	2,358	0	0.8578	0.1314	0.0101	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
19	5.0	2,358	0	0.8578	0.1314	0.0101	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
20	22.0	10,377	1	0.5093	0.3436	0.1159	0.0260	0.0044	0.0006	0.0001	0.0000	0.0000	0.0000	0.0000	0.9998
21	2.0	943	0	0.9405	0.0575	0.0018	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
22	1.5	708	0	0.9550	0.0438	0.0010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
23	2.5	1,179	0	0.9262	0.0709	0.0027	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
24	2.0	943	0	0.9405	0.0575	0.0018	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
25	8.0	3,774	0	0.7824	0.1919	0.0235	0.0019	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
26	10.0	4,717	0	0.7359	0.2256	0.0346	0.0035	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
27	13.0	6,132	0	0.6712	0.2675	0.0533	0.0071	0.0007	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
28	4.5	2,123	0	0.8711	0.1201	0.0083	0.0004	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
29	6.0	2,830	0	0.8319	0.1530	0.0141	0.0009	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
30	4.0	1,887	0	0.8846	0.1084	0.0066	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
31	3.0	1,415	0	0.9121	0.0838	0.0038	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
32	6.5	3,066	0	0.8193	0.1632	0.0162	0.0011	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
33	7.0	3,302	0	0.8068	0.1731	0.0186	0.0013	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
34	10.0	4,717	0	0.7359	0.2256	0.0346	0.0035	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
35	4.0	1,887	0	0.8846	0.1084	0.0066	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
36	1.5	708	1	0.9550	0.0438	0.0010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
37	1.5	708	0	0.9550	0.0438	0.0010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
38	4.0	1,887	0	0.8846	0.1084	0.0066	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
39	4.0	1,887	0	0.8846	0.1084	0.0066	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
40	10.0	4,717	0	0.7359	0.2256	0.0346	0.0035	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
41	8.0	3,774	0	0.7824	0.1919	0.0235	0.0019	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
42	5.0	2,358	0	0.8578	0.1314	0.0101	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
43	2.5	1,179	0	0.9262	0.0709	0.0027	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
44	2.5	1,179	0	0.9262	0.0709	0.0027	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
45	7.5	3,538	2	0.7945	0.1827	0.0210	0.0016	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
46	2.0	943	0	0.9405	0.0575	0.0018	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
47	0.5	236	0	0.9848	0.0150	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
Total	293.5	138,443	9	39.40	6.41	1.00	0.16	0.02	0.00	0.00	0.00	0.00	0.00	0.00	46.99

TABLE 4.—Data for analysis, by Chi-square contingency tests, of the integrity of schools of skipjack tuna released during tagging cruise 1079. [exp. = expected; obs. = observed.]

Date of release	Month of recapture	Tags		Occurrences of tagged fish 0	1	2	3	4	5	>5	Total	χ^2 value	df	Probability
9 June 1976	June	13	exp.	284.87	11.38	0.63	0.09	0.02			297.00	0.001	1	>0.05
		13	obs.	285	11	1					297			
10 June 1976		26	exp.	271.06	20.61	1.81	0.32	0.11	0.04	0.01	294.00	4.672	1	<0.05
		26	obs.	281	8	2	1		1	1	294			
17 June 1976		80	exp.	194.53	44.10	9.32	2.23	0.68	0.31	0.76	252.00	16.032	2	<0.01
		80	obs.	218	20	6	4			4	252			
18 June 1976		33	exp.	212.49	23.70	2.82	0.56	0.22	0.11	0.08	240.00	2.316	1	>0.05
		33	obs.	220	13	3	2	2			240			
19 June 1976		6	exp.	226.26	5.50	0.21	0.02				232.00	0.012	1	>0.05
		6	obs.	226	6						232			
Total		158	exp.	1,189.21	105.29	14.79	3.22	1.03	0.46	0.85	1,315.00	38.280	3	<0.01
		158	obs.	1,230	58	12	7	2	1	5	1,315			
9 June 1976	July	13	exp.	373.43	12.14	0.40	0.01				386.00	0.203	1	>0.05
		13	obs.	375	9	2					386			
10 June 1976		17	exp.	369.73	15.56	0.66	0.03				386.00	0.686	1	>0.05
		17	obs.	373	10	2	1				386			
17 June 1976		120	exp.	294.44	70.30	15.83	3.93	1.05	0.28	0.09	386.00	80.519	3	<0.01
		120	obs.	339	20	8	8	5	4	2	386			
18 June 1976		88	exp.	314.41	58.43	10.48	2.08	0.43	0.09	0.02	386.00	31.073	2	<0.01
		88	obs.	342	22	9	8	2	2	1	386			
19 June 1976		23	exp.	364.32	20.43	1.16	0.07				386.00	0.662	1	>0.05
		23	obs.	368	14	3	1				386			
Total		261	exp.	1,716.33	176.86	28.53	6.12	1.48	0.37	0.11	1,930.00	141.566	3	<0.01
		261	obs.	1,797	75	24	18	7	6	3	1,930			
9 June 1976	August	1	exp.	46.02	0.96	0.02					47.00			
		1	obs.	46	1						47			
10 June 1976		0	exp.	47.00							47.00			
		0	obs.	47							47			
17June 1976		9	exp.	39.40	6.41	1.00	0.16	0.02			47.00	0.402	1	>0.05
		9	obs.	41	4	1	1				47			
18 June 1976		4	exp.	43.30	3.42	0.26	0.02				47.00			
		4	obs.	44	2	1					47			
19 June 1976		1	exp.	46.02	0.96	0.02					47.00			
		1	obs.	46	1						47			
Total		15	exp.	221.74	11.75	1.30	0.18	0.02			235.00	0.408	1	>0.05
		15	exp.	224	8	2	1				235			

and observed values, and the results are shown in the last four columns of Table 4. The categories were combined so that none had an expected value of less than 5. For the first test in Table 4 (releases on 9 June 1976, and recaptures during June), for example, the expected values are 284.87 and (11.38 + 0.63 + 0.09 + 0.02 = 12.12) and the observed values are 285 and (11 + 1 = 12). When only one category had an expected value of 5 or greater no test was run.

The two total lines for each section of Table 4 are listed in Table 5, with the equivalent values for the other four experiments. These were summed for each cruise and month of recapture, and Chi-square tests were run with these sums. Those results are shown in the last four columns of Table 5.

The results of the tests are summarized as follows:

		Months of recapture					
Category	*df*	*6*	*7*	*8*	*9*	*10*	*11*
releases made on individual dates	1	3/11	2/17	0/12	0/10	0/6	
	2	1/1	3/4	0/1			
	3	1/1	2/2				
	4	2/2					
totals for cruises	1	0/1	0/2	0/4	0/2	0/3	0/2
	2		1/1	0/1	1/1		
	3	1/2	2/2				
	4	1/1					
overall totals	1					0/1	0/1
	2			1/1	1/1		
	3		1/1				
	4	1/1					

TABLE 4.—*Continued.*

Date of release	Month of recapture	Tags		Occurrences of tagged fish 0	1	2	3	4	5	>5	Total	χ^2 value	df	Probability
9 June	September	5	exp.	537.05	4.90	0.05					542.00			
1976		5	obs.	537	5						542			
10 June		8	exp.	534.12	7.75	0.12					542.00	0.002	1	>0.05
1976		8	obs.	534	8						542			
17 June		48	exp.	498.05	40.23	3.35	0.30	0.03			542.00	2.969	1	>0.05
1976		48	obs.	509	20	12		1			542			
18 June		43	exp.	502.28	36.68	2.77	0.22	0.02			542.00	0.889	1	>0.05
1976		43	obs.	508	26	7	1				542			
19 June		14	exp.	528.37	13.26	0.35	0.01				542.00	0.030	1	>0.05
1976		14	obs.	529	12	1					542			
Total		118	exp.	2,599.87	102.82	6.64	0.53	0.05			2,710.00	39.481	2	<0.01
		118	obs.	2,617	71	20	1	1			2,710			
9 June	October	3	exp.	543.02	2.96	0.02					546.00			
1976		3	obs.	544	1	1					546			
10 June		5	exp.	541.06	4.88	0.06					546.00			
1976		5	obs.	541	5						546			
17 June		31	exp.	517.04	27.07	1.74	0.13	0.01			546.00	1.766	1	>0.05
1976		31	obs.	524	15	5	2				546			
18 June		18	exp.	528.71	16.60	0.65	0.03				546.00	0.099	1	>0.05
1976		18	obs.	530	14	2					546			
19 June		4	exp.	542.04	3.93	0.04					546.00			
1976		4	obs.	542	4						546			
Total		61	exp.	2,671.87	55.44	2.51	0.16	0.01			2,730.00	1.465	1	>0.05
		61	obs.	2,681	39	8	2				2,730			
9 June	November	0	exp.	262.00							262.00			
1976		0	obs.	262							262			
10 June		1	exp.	261.00	0.99						262.00			
1976		1	obs.	261	1						262			
17 June		1	exp.	261.00	0.99						262.00			
1976		1	obs.	261	1						262			
18 June		2	exp.	260.02	1.96	0.02					262.00			
1976		2	obs.	260	2						262			
19 June		2	exp.	260.02	1.96	0.02					262.00			
1976		2	obs.	260	2						262			
Total		6	exp.	1,304.04	5.90	0.04					1,310.00	0.000	1	>0.05
		6	obs.	1,304	6						1,310			

This means that for individual dates for recaptures during June (i.e., during the month of release), 3 of 11 tests equivalent to those in Table 4 with 1 degree of freedom were significant at the 5% level; for recaptures during July, 2 of 17 tests equivalent to those in Table 4 with 1 degree of freedom were significant; and so on. From these tests it appears that after 1 month at liberty the tagged and untagged fish are randomly mixed with one another in some cases, and after 3 to 5 months at liberty they are randomly mixed with one another in nearly all cases.

Binomial Homogeneity Tests

For the binomial homogeneity test the formula

$$\chi^2 = \sum_{i=1}^{n} \frac{(T_i - F_i\hat{P})^2}{F_i\hat{P}(1 - \hat{P})}$$

where T_i = number of tagged fish in set i,
F_i = number of tagged and untagged fish in set i,
n = number of sets, and
$\hat{P}$ = probability of a fish being tagged = $\sum_{i=1}^{n} (T_i) / \sum_{i=1}^{n} (F_i)$

is used. Computer program SCHOOLA was used for this purpose.

The results are given in Table 6. In general, the

TABLE 5.—Data for analysis, by Chi-square contingency tests, of the integrity of schools of skipjack tuna released during all cruises. [exp. = expected; obs. = observed.]

Tagging cruise	Month of recapture	Tags		Occurrences of tagged fish 0	1	2	3	4	5	>5	Total	χ^2 value	df	Probability
1042	June	439	exp.	971.84	193.13	53.10	19.75	8.53	3.89	4.76	1,255.00	121.553	4	<0.01
		439	obs.	1,114	74	26	11	4	7	19	1,255			
1043		130	exp.	203.70	39.03	11.32	4.42	2.08	1.16	4.29	266.00	5.428	3	>0.05
		130	obs.	212	27	11	8	3	3	2	266			
1070		7	exp.	345.25	6.51	0.23	0.01				352.00	0.009	1	>0.05
		7	obs.	345	7						352			
1079		158	exp.	1,189.21	105.29	14.79	3.22	1.03	0.46	0.85	1,315.00	38.280	3	<0.01
		158	obs.	1,230	58	12	7	2	1	5	1,315			
Total		734	exp.	2,710.00	343.96	79.44	27.40	11.64	5.51	9.90	3,188.00	149.523	6	<0.01
		734	obs.	2,901	166	49	26	9	11	26	3,188			
1042	July	152	exp.	1,265.04	107.21	15.36	3.20	0.75	0.17	0.27	1,392.00	32.137	2	<0.01
		152	obs.	1,307	55	22	4	0	1	3	1,392			
1043		248	exp.	1,479.32	158.72	26.60	6.72	2.19	0.79	0.44	1,675.00	50.425	3	<0.01
		248	obs.	1,536	96	18	12	6	2	5	1,675			
1070		32	exp.	545.75	28.57	1.54	0.09				576.00	0.002	1	>0.05
		32	obs.	546	28	2					576			
1075		13	exp.	338.04	11.01	0.84	0.09				350.00	2.130	1	>0.05
		13	obs.	343	6					1	350			
1079		261	exp.	1,716.33	176.86	28.53	6.12	1.48	0.37	0.11	1,930.00	141.566	3	<0.01
		261	obs.	1,797	75	24	18	7	6	3	1,930			
Total		706	exp.	5,344.48	482.37	72.87	16.22	4.42	1.33	0.82	5,923.00	231.819	4	<0.01
		706	obs.	5,529	260	66	34	13	9	12	5,923			
1042	August	44	exp.	2,613.04	41.88	0.98	0.03				2,656.00	0.582	1	>0.05
		44	obs.	2,618	33	4	1				2,656			
1043		108	exp.	2,211.08	90.80	7.13	0.78	0.10	0.01		2,310.00	2.334	2	>0.05
		108	obs.	2,219	80	7	3		1		2,310			
1070		15	exp.	465.42	14.16	0.39					480.00	0.012	1	>0.05
		15	obs.	465	15						480			
1075		55	exp.	1,044.57	48.13	2.92	0.26	0.03			1,096.00	0.602	1	>0.05
		55	obs.	1,050	39	5	2				1,096			
1079		15	exp.	221.74	11.75	1.30	0.18	0.02			235.00	0.408	1	>0.05
		15	obs.	224	8	2	1				235			
Total		237	exp.	6,555.85	206.72	12.72	1.25	0.15	0.01		6,777.00	14.206	2	<0.01
		237	exp.	6,576	175	18	7		1		6,777			
1043	September	39	exp.	2,290.28	36.42	1.18	0.05				2,328.00	0.014	1	>0.05
		39	obs.	2,291	35	2					2,328			
1070		27	exp.	156.88	19.77	2.88	0.41	0.05			180.00	0.483	1	>0.05
		27	obs.	160	14	5	1				180			
1079		118	exp.	2,599.87	102.82	6.64	0.53	0.05			2,710.00	39.481	2	<0.01
		118	obs.	2,617	71	20	1	1			2,710			
Total		184	exp.	5,047.03	159.01	10.70	0.99	0.10			5,218.00	36.868	2	<0.01
		184	obs.	5,068	120	27	2	1			5,218			
1043	October	13	exp.	1,481.38	12.26	0.35	0.01				1,494.00	0.031	1	>0.05
		13	obs.	1,482	11	1					1,494			
1070		33	exp.	788.27	30.49	1.17	0.04				820.00	0.017	1	>0.05
		33	obs.	789	29	2					820			
1079		61	exp.	2,671.87	55.44	2.51	0.16	0.01			2,730.00	1.465	1	>0.05
		61	obs.	2,681	39	8	2				2,730			
Total		107	exp.	4,941.52	98.19	4.03	0.21	0.01			5,044.00	1.094	1	>0.05
		107	obs.	4,952	79	11	2				5,044			
1070	November	10	exp.	906.14	9.69	0.14					916.00	0.002	1	>0.05
		10	obs.	906	10						916			
1079		6	exp.	1,304.04	5.90	0.04					1,310.00	0.000	1	>0.05
		6	obs.	1,304	6						1,310			
Total		16	exp.	2,210.18	15.59	0.18					2,226.00	0.002	1	>0.05
		16	obs.	2,210	16						2,226			

χ^2/df values do not appear to decrease consistently with time, as would be expected if the fish tend to mix gradually with time. If, however, only the values corresponding to date of release-month of recapture strata with more than 10 tag returns are considered the χ^2/df values tend to decrease with time. The χ^2 values corresponding to these strata are summed at the bottoms of the first five sections of Table 6, and these sums are divided by the sums of the degrees of freedom to obtain total χ^2/df values. It can be seen that these also tend to decrease with time. In addition, the χ^2 values and degrees of freedom for the strata with more than 10 tag returns for all the experiments are summed in the last section of Table 6; the χ^2/df values again tend to decrease with time. It thus appears that the fish were gradually mixing as time passed.

One thousand Monte Carlo simulations were run for each stratum with more than 10 tags, using computer program MONTCARL, to determine the probability of obtaining an equal or greater value of χ^2/df, if the tagged and untagged fish were randomly mixed with one another. The results are shown in the last column of Table 6. In most cases these indicated that the tagged and untagged fish were not randomly mixed. These data tend to indicate less rapid mixing with time than do the data for the Chi-square contingency tests.

DISCUSSION

There is a fundamental difference between the two methods. The Chi-square contingency tests test whether the tagged fish occurred in many or few of the schools, whereas the binomial tests test whether the ratios of tagged to total fish are consistent among schools. For example, if there was a total of 15 returns of tagged fish obtained from 15 different sets from a total of 20 25-ton sets and 20 1-ton sets, it would make no difference for the Chi-square contingency tests which sets the tagged fish occurred in. For the binomial homogeneity tests, however, the χ^2/df value would be much greater if the tagged fish occurred in 15 of the 20 1-ton sets than if they occurred in 15 of the 20 25-ton sets.

The Chi-square contingency tests are adversely affected by the small numbers of tag returns, which makes them rather low powered. For example, for the releases of 19 June 1962, and 28 June 1963,

TABLE 6.—Results of binomial homogeneity tests with skipjack tuna tag return data.

Year	Date of release	Month of recapture	Sets	Tags	χ^2	χ^2/df	Probability
1962	2 June	June	228	33	714.44	3.15	<0.01
		July	174	15	236.33	1.37	>0.05
		August	333	10	1,467.22	4.42	
	3 June	June	223	26	880.38	3.97	<0.01
		July	174	18	272.03	1.57	<0.05
		August	333	10	304.10	0.92	
	4 June	June	212	32	4,395.24	20.83	<0.01
		July	174	15	327.12	1.89	<0.05
		August	333	9	666.62	2.01	
	17 June	June	162	129	7,862.99	48.84	<0.01
		July	174	6	333.26	1.93	
		August	333	1	81.91	0.25	
	18 June	June	152	15	435.92	2.89	<0.01
		July	174	2	466.73	2.70	
		August	333	0	—	—	
	19 June	June	141	95	543.94	3.89	<0.01
		July	174	28	575.73	3.33	<0.01
		August	333	5	236.97	0.71	
	23 June	June	77	95	392.78	5.17	<0.01
		July	174	40	744.76	4.30	<0.01
		August	333	7	533.24	1.61	
	24 June	June	60	14	99.18	1.68	<0.05
		July	174	28	1,592.40	9.20	<0.01
		August	333	2	299.98	0.90	
	Total	June	1,255	439	15,324.87	12.29	
		July	1,044	144	3,748.37	3.61	

TABLE 6.—*Continued.*

Year	Date of release	Month of recapture	Sets	Tags	χ^2	χ^2/df	Probability
1963	5 June	June	89	26	141.07	1.60	>0.05
		July	282	25	702.74	2.50	<0.01
		August	385	16	1,250.94	3.26	<0.01
		September	388	6	645.62	1.67	
		October	249	1	2,110.73	8.51	
	9 June	June	89	28	293.56	3.34	<0.01
		July	282	50	1,036.42	3.69	<0.01
		August	385	24	514.06	1.34	>0.05
		September	388	6	779.54	2.01	
		October	249	2	314.69	1.28	
	20 June	June	53	12	56.66	1.09	>0.05
		July	282	15	532.52	1.90	<0.05
		August	385	10	681.99	1.78	
		September	388	6	1,105.22	2.86	
		October	249	2	192.00	0.78	
	27 June	June	24	33	197.47	8.59	<0.01
		July	282	101	1,683.31	5.99	<0.01
		August	385	48	1,019.23	2.65	<0.01
		September	388	19	843,91	2.18	<0.01
		October	249	8	258.17	1.05	
	28 June	June	11	31	401.40	40.14	<0.01
		July	282	43	1,071.63	3.81	<0.01
		August	385	5	85.27	0.22	
		September	388	1	268.06	0.69	
		October	249	0	—	—	
	1 July	July	265	14	1,272.38	4.82	<0.01
		August	385	5	1,000.85	2.61	
		September	388	1	447.33	1.16	
		October	249	0	—	—	
	Total	June	266	130	1,090.16	4.16	
		July	1,675	248	6,299.00	3.77	
		August	1,155	88	2,784.23	2.42	
		September	388	19	843.91	2.18	
1973	12 June	June	129	4	125.55	0.98	
		July	144	9	190.46	1.33	
		August	120	4	90.50	0.76	
		September	45	5	77.04	1.75	
		October	205	7	289.43	1.42	
		November	229	1	78.43	0.34	
	13 June	June	118	3	156.86	1.34	
		July	144	8	118.45	0.83	
		August	120	4	256.57	2.16	
		September	45	4	24.50	0.56	
		October	205	13	214.15	1.05	>0.05
		November	229	3	116.14	0.51	
	14 June	June	105	0	—	—	
		July	144	6	333.14	2.33	
		August	120	2	78.99	0.66	
		September	45	8	41.23	0.94	
		October	205	10	387.81	1.90	
		November	229	5	477.96	2.10	
	30 June	July	144	9	344.95	2.41	
		August	120	5	50.35	0.42	
		September	45	10	21.62	0.49	
		October	205	3	324.07	1.59	
		November	229	1	197.57	0.87	
	Total	October	205	13	214.15	1.05	

TABLE 6.—*Continued.*

Year	Date of release	Month of recapture	Sets	Tags	χ^2	χ^2/df	Probability
1975	26 June	July	215	5	192.62	0.90	
		August	274	15	536.17	1.96	<0.01
	20 July	July	51	1	13.23	0.26	
		August	274	8	246.67	0.90	
	21 July	July	42	7	64.87	1.58	
		August	274	10	1,255.33	4.60	
	21 July	July	42	0	—	—	
		August	274	22	1,036.53	3.80	<0.01
	Total	August	548	37	1,572.70	2.88	
1976	9 June	June	297	13	468.83	1.58	>0.05
		July	386	13	874.92	2.27	<0.01
		August	47	1	38.13	0.83	
		September	542	5	628.52	1.16	
		October	546	3	1,830.07	3.36	
		November	262	0	—	—	
	10 June	June	294	26	664.08	2.27	<0.01
		July	386	17	744.88	1.93	<0.01
		August	47	0	—	—	
		September	542	8	578.70	1.07	
		October	546	5	354.91	0.65	
		November	262	1	410.61	1.57	
	17 June	June	252	80	977.05	3.89	<0.01
		July	386	120	1,283.42	3.33	<0.01
		August	47	9	359.63	7.82	
		September	542	48	1,448.02	2.68	<0.01
		October	546	31	1,002.48	1.84	<0.01
		November	262	1	153.34	0.59	
	18 June	June	240	33	1,749.76	7.32	<0.01
		July	386	88	947.11	2.46	<0.01
		August	47	4	399.34	8.68	
		September	542	43	2,018.78	3.73	<0.01
		October	546	18	704.02	1.29	>0.05
		November	262	2	105.17	0.40	
	19 June	June	232	6	249.12	1.08	
		July	386	23	611.28	1.59	<0.05
		August	47	1	292.31	6.35	
		September	542	14	594.33	1.10	>0.05
		October	546	4	771.34	1.42	
		November	262	2	242.38	0.93	
	Total	June	1,083	152	3,859.72	3.58	
		July	1,930	261	4,461.61	2.32	
		September	1,626	105	4,061.13	2.50	
		October	1,092	49	1,706.50	1.57	
all		June	2,604	721	20,274.75	7.84	
		July	4,649	653	14,508.98	3.13	
		August	1,703	125	4,356.93	2.56	
		September	2,014	124	4,905.04	2.44	
		October	1,297	62	1,920.65	1.48	

there were sets with more than five tagged fish in them, and yet the results of the Chi-square tests were not significant. This is caused by the requirement that each category have an expected value of 5 or greater. Accordingly, it is likely that if there had been more tag returns, there would have been more categories for many of the tests and significant results for more of them. The practice of combining the results for fish of the same experiment released on different days ("Total" lines in Table 4) and for fish of different experiments ("Total" lines of Table 5) helps to overcome this weakness. It can be seen in the text table above that the ratios increased with the degrees of freedom. If there were more tag returns, there would be fewer tests with one degree of freedom and more with three or more degrees of freedom, and the ratios of significant tests would almost certainly increase.

On the other hand, the way that the tag return data are handled causes it to appear that there were more sets with more than one tagged fish than was actually the case. Ideally, all tagged fish would be recovered by fishermen as soon as they are caught, and then set aside for later examination by an IATTC employee, and the tag numbers, locations, and dates of recapture would be recorded so that each fish could be assigned to the proper set. In reality, however, less than half the tagged fish recaptured are recovered by the fishermen, and since the fish from different sets are mixed in the wells of the vessels, the chance of assigning tagged fish to specific sets is lost, except when enough fish are caught in one set to fill an entire well. Virtually all of the tagged fish which are not recovered by fishermen are recovered later by unloaders and cannery workers. The unloaders and cannery workers usually inform the IATTC employee to whom they return the tagged fish (or the tag without the fish attached to it) that the fish was found in or had come from a particular well or pair of wells of a particular boat. The IATTC employee who receives the tagged fish or tag records this information, and later another IATTC employee compares this information with an abstract of the vessel's logbook and assigns the fish to the set which contributed the greatest weight of fish of the species in question to that well or pair of wells. For example, if a particular well contained fish from sets with 12, 15, 20, and 13 tons made on 1, 2, 3, and 4 June, respectively, and each included one tagged fish, all recovered by unloaders and cannery workers, all four would be assigned to the 3 June set. This would make it appear that the tagged fish tend to remain together more than is actually the case. Another way to handle a situation such as this would be to allocate the four fish among the four sets in proportion to the weights of fish in them, in this case one to each set. This is not done, however, because tagged fish from the same trip of the same vessel are often returned to the IATTC over a considerable period of time, and it is not feasible to keep the tags for long periods waiting for all of them to be returned before processing them. Furthermore, allocation of tagged fish in the way just described would tend to make it appear that the tagged fish remain together less than they actually do if they are not randomly mixed with the untagged ones.

In addition to the problems created by failure to recover all the tagged fish as soon as they are caught, there are probably problems created by false data. Sometimes the persons recovering tagged fish keep the tags they have recovered over a period of several days, weeks, or even longer, and then return them to an IATTC employee, telling him that they were all recovered that day in the well or pair of wells that was unloaded that day. The likelihood that the data are false can often, but not always, be detected by an alert IATTC employee. When the likelihood that the data are false is not detected, it will appear that the tagged fish remain together more than is actually the case. It is believed that, in spite of attempts to detect data which are likely to be false, some false data are included in the analyses and make it appear that the tagged fish remain together more than is actually the case.

The fact that the numbers of tag returns were small, coupled with the requirement for the Chi-square contingency tests that the categories for the expected numbers of tagged fish be equal to or greater than 5, tends to make it appear that the tagged fish mix more rapidly with the untagged ones than is actually the case. The biases resulting from the mixing of the fish caught in different sets in the same wells and from false data tend to make it appear that the tagged and untagged fish mix less rapidly than is actually the case. Thus the two factors tend to cancel each other out, at least partially, although the first bias may be stronger than the second. If so, the tentative conclusion made above that the tagged and untagged fish mix thoroughly within about 3 to 5 months may be incorrect; that time could be somewhat longer. For the binomial homogeneity tests only the second bias exists, so the rate of mixing of the tagged and untagged fish indicated by these tests is probably somewhat slower than is actually the case.

Sharp (1978) stated that it is likely that skipjack tuna in the same school are "related," but it seems unlikely that tunas could school together for their entire lives, an implication attributed to Sharp (1978) by Lester et al. (1985). During the egg and larval stages, the fish are at the mercy of their environment, and individuals which were together at one time would often be separated by the currents. Furthermore, large tunas of the genus *Thunnus* occur mostly in subsurface waters at depths to nearly 300 m (Suzuki et al. 1977). Although there are areas of greater and lesser concentrations of large, subsurface-dwelling fish, there is no evidence that they form concentrated schools such as those which occur at the surface. The present study indicates that skipjack tuna in the size range of about 3.4 to 7.0 pounds (about 43 to 53 cm in length) of the same school mix randomly with those of other schools

within about 3 to 5 months, or possibly somewhat longer. This is in agreement with the findings of Anonymous (1960) and Lester et al. (1985), but not those of Sharp (1978), discussed at the beginning of this report.

ACKNOWLEDGMENTS

Appreciation is expressed to Gayle Ver Steeg, who compiled the catch and effort data; to Stephen T. Buckland, Richard G. Punsly, and Patrick K. Tomlinson, who contributed some ideas for analysis of the data; and to Stephen T. Buckland, Andrew E. Dizon, Ashley J. Mullen, Richard G. Punsly, Michael D. Scott, and three anonymous reviewers, who made some useful suggestions for improvement of the manuscript.

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COMPARISON OF TWO LENGTH-FREQUENCY BASED PACKAGES FOR ESTIMATING GROWTH AND MORTALITY PARAMETERS USING SIMULATED SAMPLES WITH VARYING RECRUITMENT PATTERNS

MARGARIDA CASTRO AND KARIM ERZINI[1]

ABSTRACT

Length-frequency distributions were simulated for species with recruitment patterns characteristic of many tropical fish: 1) one recruitment peak per year, fast growth and very high mortality, 2) one recruitment peak per year, slow growth and moderate to high mortality, 3) two recruitment peaks per year, slow growth and moderate to high mortality, and 4) random recruitment, slow growth and moderate to high mortality. Two microcomputer program packages—one incorporating the ELEFAN I & II programs and the other implementing a form of Modal Progression Analysis—were used to estimate growth and mortality parameters, and these were compared with the initial parameters used to generate the simulated samples. The results, while generally encouraging, suggest that multiple recruitments per year make it difficult to estimate growth and mortality parameters using these two packages.

Information concerning growth, mortality, and recruitment patterns is of great importance in length-frequency analysis. The purpose of this paper was to evaluate two sets of methods used in length-frequency analysis in terms of their ability to produce accurate estimates of growth and mortality parameters in the absence of such biological information.

The methodology chosen consisted of generation of length-frequency distributions with known parameters to which the length-frequency methods were applied. The results obtained with the method were compared with the initial conditions. This procedure has been used in other studies (Hampton and Majkowski 1987; Jones 1987).

The development of the program for simulating length frequencies was guided by assumptions implicit in the length-frequency methods and by known factors concerning the biology of fish. These include 1) average individual growth in accordance with the von Bertalanffy growth curve, 2) little variation in natural mortality throughout the exploited phase, 3) exponential decline in the numbers of a cohort, 4) length distributions normal for each age class, and 5) recruit numbers random. Some other features of the program, such as the selectivity of the gear (logistic type) are not standard assumptions of length-frequency methods but are options for parameters necessary to describe the effect of fishing.

The authors believe that the simulated length frequencies accurately reflect the assumptions of the length-frequency methods and therefore the generated samples can be used to test, correct, and possibly improve these methods. The simulated samples might also help to define a range of situations when a specific length-frequency method can or cannot be used.

Traditionally, length-frequency analysis methods have been used as validation methods for age determinations made independently. Recently, these techniques have grown in importance and frequency of use, in particular in tropical fisheries, where age determinations based on direct reading of check marks in hard parts of the fish are difficult, and in crustaceans, which do not have permanent hard structures. As a result, length-frequency analysis has been used in situations where very little is known about the biology of the species.

It is the purpose of this work to contribute to the understanding of the possible errors that are made when length-frequency analysis is used without biological information on mortality levels, growth parameters, and, in particular, recruitment patterns. It might be argued that such methods of length-frequency analysis are particularly useful in the situations described above, precisely because they do not require a priori knowledge of biological information. The question then becomes, is it legitimate to use length-frequency analysis techniques in the absence of minimum biological information? And if the answer to this question is no, then what

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Manuscript accepted July 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

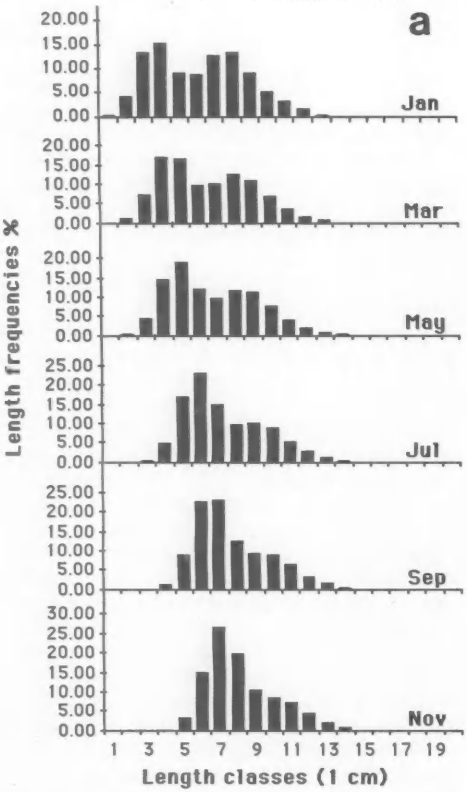
are the minimum requirements for each one of the length-frequency analysis methods? We hope this paper can contribute to providing some understanding of this problem.

MATERIALS AND METHODS

The Simulation Program: SIMULPOP[2]

SIMULPOP was developed in BASIC, for IBM microcomputers and compatibles. Populations are simulated by following cohorts in time and the general characteristics and assumptions of the program include 1) individual growth described by a von Bertalanffy growth curve, no seasonality considered; 2) recruitment: different patterns and random in numbers; 3) natural mortality: random and normally distributed; 4) fishing mortality: random and normally distributed, and corrected for incomplete selectivity in younger ages; 5) selectivity: logistic equation considered to represent selectivity of the fishing gear; and 6) length distribution for each age normally distributed, with a mean given by the von Bertalanffy growth curve. The shapes of the frequency distributions are independent of

[2]The program SIMULPOP is available from Margarida Castro upon request.



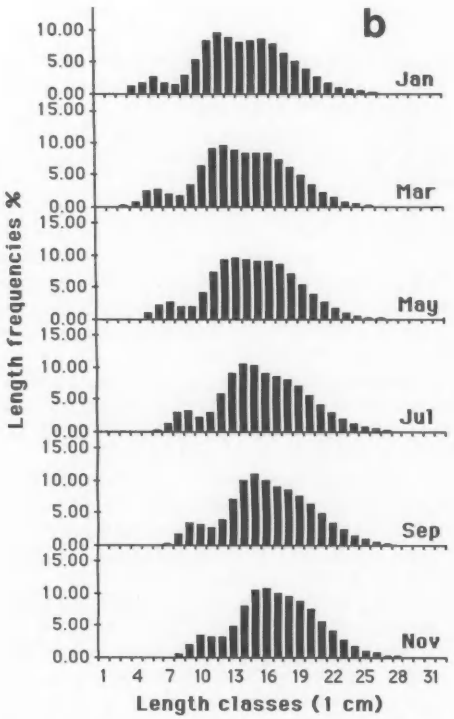


FIGURE 1a.—Example of simulated length-frequency distributions for situation 1, the sardine-type species with one recruitment peak a year. Only 6 of the 12 months are represented.

FIGURE 1b.—Example of simulated length-frequency distributions for situation 2, the sparid/lutjanid-type species with one recruitment peak a year. Only 6 of the 12 months are represented.

catch size and can be regarded as unbiased. Examples of simulated length frequencies for each of the four situations are presented in Figures 1a–d and examples of component distributions contributing to the composition of a particular distribution are given in Figures 2a–d. In what follows, the word cohort refers to the fish recruited in a particular period. For one spawning peak a year cohort and age class are equivalent. However, in the situations where multiple recruitment periods were simulated, more than one cohort will contribute to a given age class. In multiple recruitment situations the word cohort does not have its traditional meaning.

The Choice of Parameters

The following four situations were simulated and the parameters are given in Table 1: 1) A sardine-like species, characterized by small size, fast growth, high mortality, very intense fishing mortality, and with one recruitment peak per year (situation 1); 2) a small sparid/lutjanid type species, with larger size, slower growth with moderate to high fishing mortality, and one recruitment peak per year (situation 2); 3) a species with the same characteristics as the one described previously, but with two recruitment peaks per year (situation 3); and 4) a species with the same characteristics as the two

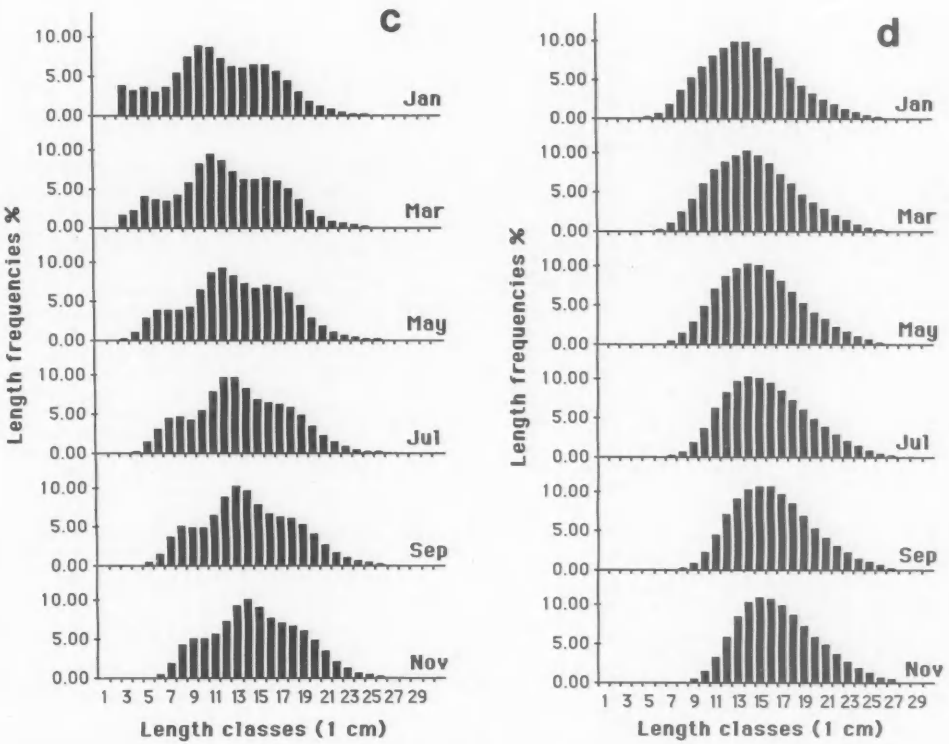
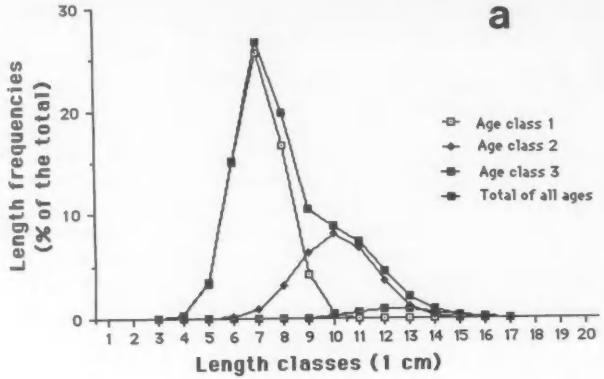


FIGURE 1c.—Example of simulated length-frequency distributions for situation 3, the sparid/lutjanid-type species with two recruitment peaks a year. Only 6 of the 12 months are represented.

FIGURE 1d.—Example of simulated length-frequency distributions for situation 4, the sparid/lutjanid-type species with random recruitment. Only 6 of the 12 months are represented.



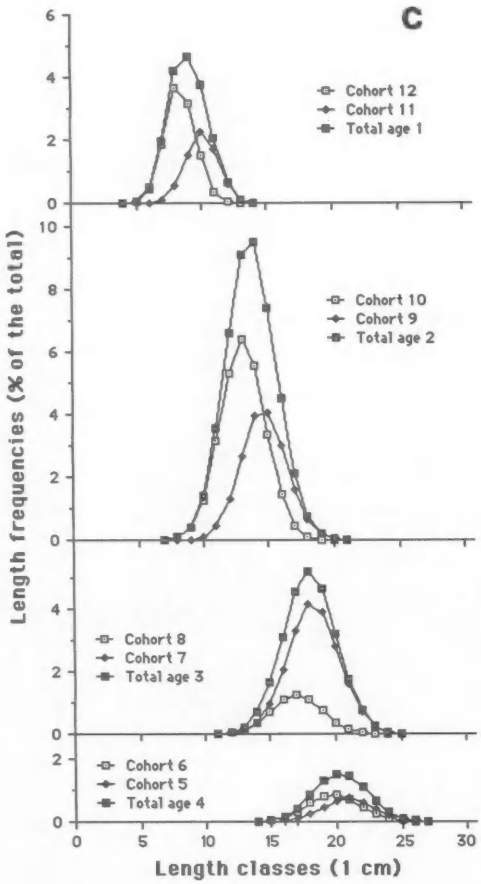
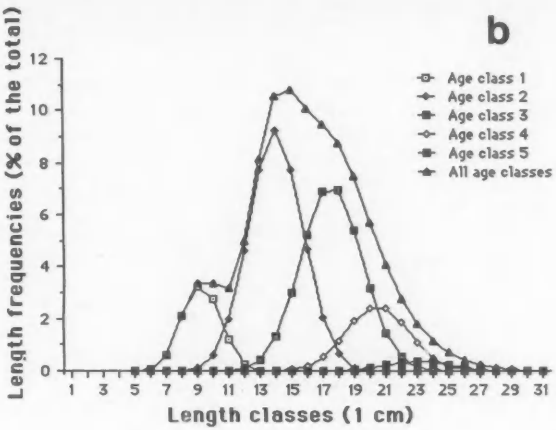


FIGURE 2a.—Example showing component distributions for one length-frequency sample (month of November of the same simulation represented in Figure 1a) for situation 1. Age class 4 is not represented due to low frequencies.

FIGURE 2b.—Example showing component distributions for one length-frequency sample (month of November of the same simulation represented in Figure 1b) for situation 2. Age class 6 is not represented due to low frequencies.

FIGURE 2c.—Example showing component distributions for one length-frequency sample (month of November of the same simulation represented in Figure 1c) for situation 3. There are two cohorts contributing to each age class. Ages 5 and 6 are not represented due to low frequencies.

FIGURE 2d.—Example showing component distributions for one length-frequency sample (month of November of the same simulation represented in Figure 1d) for situation 4. In this case there are multiple cohorts contributing to each age class. Age classes 1 and 6 are not represented due to low frequencies.


b
Length frequencies (% of the total)
Length classes (1 cm)
Age class 1
Age class 2
Age class 3
Age class 4
Age class 5
All age classes

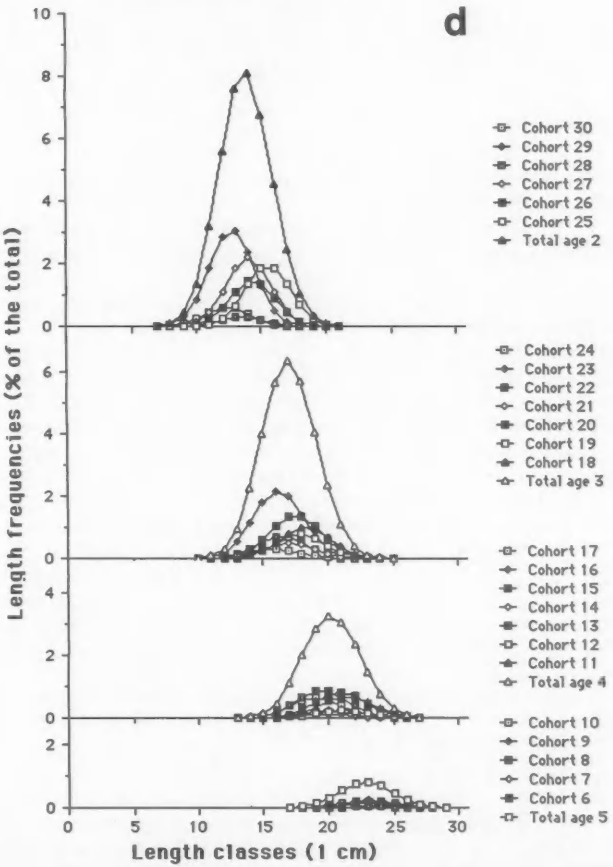

d
Length frequencies (% of the total)
Length classes (1 cm)
Cohort 30
Cohort 29
Cohort 28
Cohort 27
Cohort 26
Cohort 25
Total age 2
Cohort 24
Cohort 23
Cohort 22
Cohort 21
Cohort 20
Cohort 19
Cohort 18
Total age 3
Cohort 17
Cohort 16
Cohort 15
Cohort 14
Cohort 13
Cohort 12
Cohort 11
Total age 4
Cohort 10
Cohort 9
Cohort 8
Cohort 7
Cohort 6
Total age 5

TABLE 1.—Parameters chosen for the simulations.

Situation:	1	2	3	4
Oldest age present in catch (years)	4	6	6	6
Age of recruitment to the area of adult stock (months)	6	6	6	6
Growth parameters				
L_∞ (cm)	20	35	35	35
K	0.3	0.2	0.2	0.2
t_0 (years)	0	0	0	0
Instantaneous annual natural mortality rate				
Mean	0.4	0.25	0.25	0.25
SD	0.015	0.01	0.01	0.01
Instantaneous annual fishing mortality rate				
Mean	1.7	0.8	0.8	0.8
SD	0.05	0.02	0.02	0.02
Selectivity parameters (cm)				
Mesh	1.5	3.5	3.5	3.5
Length 25% retension	3.25	11.25	11.25	11.25
Length 75% retension	8.75	16.75	16.75	16.75
Standard deviations of length-at-age				
Age 0	0.5	1.0	1.0	1.0
Age 1	1.0	1.2	1.2	1.2
Age 2	1.5	1.5	1.5	1.5
Age 3	1.5	2.0	2.0	2.0
Age 4	1.5	2.0	2.0	2.0
Age 5		2.0	2.0	2.0
Age 6		2.0	2.0	2.0
Recruitment pattern	once/yr May-June	once/yr May-June	twice/yr Mar.-Apr. Sept.-Oct.	stochastic

previous ones, but with stochastic recruitment, and random recruitment intensities assigned to randomly selected months (situation 4).

The choice of these recruitment patterns was based on the knowledge that tropical species have different types of recruitment periodicities with varying temporal and spatial variation (Thresher 1984). The same species may have different patterns (Sale et al. 1984). Two principal peaks and year-round recruitment have been reported in coral reef fish from Hawaii (Walsh 1987) and Curaçao (Luckhurst and Luckhurst 1977). One single recruitment per year has also been reported (Li 1960; Gladstone and Westoby 1988).

Mortality values, both natural and fishing, were chosen to have small standard deviations (Table 1) because the main objective was to examine the effects of different recruitment patterns, and we wanted to keep the possible effects of variations in other factors as small as possible.

The standard deviations of length-at-age used (Table 1) are representative of values for species with life history characteristics similar to those of the cases considered for this study (K. Erzini, work in progress).

The Length-Frequency Analysis

The two techniques chosen to represent length-frequency analysis were ELEFAN (Electronic Length Frequency Analysis) (Brey and Pauly 1986) and the package entitled "Length Frequency Based Fish Stock Assessment Microcomputer Programs" (LFSA package) by Sparre (1986; adapted to MS DOS by K. Erzini). ELEFAN has been widely used in the analysis of tropical fish stocks, and its non-parametric basis for determination of K and L_∞ makes it a unique methodology for the analysis of length frequencies.

In ELEFAN, the length-frequency samples are restructured in order to emphasize peaks. Details of the restructuring methodology are given in Brey and Pauly (1986). Growth curves are generated for values of K and L_∞ within specified ranges and fit to the reconstructed length-frequency data. The best curves are considered to be the ones that pass through the most peaks and the least troughs.

The LFSA package uses a method of a different nature—the Bhattacharya method (Bhattacharya 1967), to separate normal curves, under the assumption that the length distributions for each age are

normal. The decomposition of each length-frequency sample into component distributions is carried out by plotting a logarithmic transformation of the differences between successive length frequencies. A normal distribution appears as a series of values making up a straight line with a negative slope. In the LFSA package, which implements the Bhattacharya (1967) method, the user selects the points believed to make up a normal distribution, and the mean, standard deviation and various other statistics are computed. In the next step, the means of all distributions are plotted against time and the mean lengths thought by the user to reflect the progression of a cohort are linked. Finally, growth parameters are computed from the linked modes by a method referred to as a Gulland and Holt plot (Gulland and Holt 1959).

In both packages, the growth parameters are used to create age based catch curves for estimation of instantaneous annual total mortality, Z. Therefore, except for the estimation of Z, the methodologies of the two packages are quite independent. However they are both characterized by a certain degree of subjectivity.

Methodology

Following the suggestion of Hampton and Majkowski (1987), two different teams were formed. One (team A) created the simulated samples (10 cases of 12 monthly samples for each situation), and another (team B) ran the length-frequency analysis. The 40 cases were given arbitrary filenames and were mixed by team A prior to analysis by team B. This was done to avoid influencing the choice of initial values or parameter ranges, required by some of the methods applied. In estimating the growth parameters using the LFSA package, constraints on the limit of acceptable estimates of L_∞ were guided by the value of the midpoint of the largest size class in each particular case. For analysis by ELEFAN I & II, the size of the largest length class also helped guide the choice of range of potential values of L_∞. Team A provided information to team B in different phases. In phase 1, samples were provided to team B with information on mesh size, and only broad descriptions of the type of species, and indications of fishing mortality levels. Team B analyzed the length-frequency samples with both packages to the best of his ability. In Phase 2, exact information on growth, mortality, and number of age classes was provided and new estimates of Z were obtained using both packages. The results produced by team B are presented in Table 2.

It should be noted that expected values for Z in Table 2 are less than the sums of F and M in Table 1. This is because Table 1 values are inputs, and F is subsequently corrected for selectivity.

RESULTS

In situation 1, the sardine-type species with one recruitment peak per annum, the samples were simulated using growth parameters typical of a small clupeid with high fishing effort expressed by a high value of F and small mesh size. Thus a typical length-frequency sample consists of 4 component distributions or 4 cohorts (Figure 2a). While estimates of the growth parameters by ELEFAN were very good, the LFSA package estimates of K were surprisingly high.

Close examination of the length frequencies, the Bhattacharya method and Gulland and Holt plot implemented by Sparre revealed a number of factors

TABLE 2.—Results of estimation of growth and mortality parameters (mean and standard deviation) using ELEFAN and LFBFSA packages. Z_1 and Z_2 are total mortalities calculated using estimated and actual K and L_∞ values.

		ELEFAN				LFBFSA				Expected values		
Situation	Parameters	K	L_∞	Z_1	Z_2	K	L_∞	Z_1	Z_2	K	L_∞	Z
1	Mean	0.30	21.3	2.09	1.78	0.46	21.0	3.01	1.96	0.3	20.0	1.32
	SD	0.03	1.30	0.41	0.26	0.14	3.55	0.67	0.25			
2	Mean	0.18	38.8	1.35	1.22	0.18	33.2	0.89	1.17	0.2	35.0	1.02
	SD	0.02	3.10	0.27	0.14	0.06	2.97	0.33	0.22			
3	Mean	0.19	37.9	1.24	1.17	0.14	36.1	0.79	1.09	0.2	35.0	1.02
	SD	0.03	2.33	0.27	0.18	0.05	3.84	0.38	0.13			
4	Mean	0.19	37.2	1.24	1.15	0.20	36.2	1.15	1.14	0.2	35.0	1.02
	SD	0.04	2.93	0.40	0.20	0.06	4.35	0.20	0.11			

contributing to the high estimates of K. First, the relatively fast growth rate and high mortality resulted in early overlapping or accumulation of distributions and in large fish being rare so that team B could never identify more than 3 out of 4 modes corresponding to fished age classes using the Bhattacharya method in any sample (Fig. 2a). Second, the third mode was consistently overestimated because the distributions for age classes 3 and 4 were merged together. Third, the young-of-the-year fish do not appear in the samples as a well-defined distribution until late in the monthly time series of samples because recruitment does not take place until June. Finally, we found that estimates of K using the Gulland and Holt plot in the LFSA package were very sensitive to small deviations in the estimates of modal lengths obtained using the Bhattacharya method.

Total mortality estimates for situation 1 using the estimated K and L_∞ values were not good for either package. Estimates of Z using the actual K and L_∞ values used in the simulations were within 35% and 45% of the expected Z (Table 2).

Situation 2 was the sparid/lutjanid type, characterized by a single recruitment peak per year and 5 distributions corresponding to the 5 fished cohorts in the catch (Fig. 2b). Both methodologies gave similar estimates of K, close to the actual value. However, L_∞ was overestimated by ELEFAN and underestimated by the LFSA package. The mean estimate of Z was within 32% of the expected Z for the ELEFAN catch curve analysis and within 13% for the LFSA package analysis. Mean Phase II estimates of Z were 20% and 15% above the expected Z (Table 2).

Situation 3, the sparid/lutjanid type with two recruitment peaks per year (Fig. 2c) produced good results using ELEFAN. However, modal progression estimates of K were low, with corresponding underestimates of Z (Table 2). Component distributions were poorly defined compared to situation 2; age classses 4 and 5 were often obscured by the age class 3 distribution. Incorrect separation of distributions and bad estimates of growth parameters were therefore not unexpected.

For the last situation, the sparid/lutjanid type with stochastic recruitment (Fig. 2d), estimates of K, L_∞, and Z were generally good for both packages. However, as shown by the standard deviations, the range of estimates for certain parameters was quite high. This was the case for K estimated by ELEFAN and L_∞ estimated by modal progression analysis in the LFSA package.

DISCUSSION

This preliminary study has shown that, as expected, the structure of the data has a big effect on the estimates derived using length-frequency packages. In general, the results were encouraging. However, it should be noted that the simulated length-frequency distributions can be regarded as representing high-quality samples of the hypothetical populations in terms of lack of bias, sample size, and frequency of sampling. In other words, real life length-frequency data is seldom of this quality.

The modal progression analysis implemented by Sparre (1986) was more sensitive to the structure of the length-frequency samples. Worst results in terms of estimation of growth parameters were obtained under multiple recruitment (situation 3) and fast growth and high mortality (situation 1). A fundamental problem with the Bhattacharya method is the inability to identify modes at the upper end of the size spectrum, particularly when there is fast growth or many age groups. Identification of modes using the Bhattacharya method might have been improved by using smaller size class intervals, particularly for situation 1. However, even when there was little ambiguity in the selection of modes using the Bhattacharya method, it was found that the Gulland and Holt plot for estimating K and L_∞ was very sensitive to small underestimates and overestimates of the modes considered to represent growth over time.

Length converted catch curve estimates of total mortality are highly dependent on the estimated growth parameters. Consequently, estimates of Z generally paralleled estimates of K and L_∞ and were not as good as estimates of Z obtained using the actual simulation values of K. These latter estimates of Z were generally close to actual Z values for all situations despite the fact that the length-frequency data necessarily did not meet steady-state assumptions because of variable recruitment and mortality. However, the variability of mortality rates was deliberately kept small because the primary objective was to examine the effects of different recruitment patterns.

ELEFAN, the Bhattacharya, and the modal progression method of the LFSA package all require subjective decision making by the user. It would seem that ELEFAN is less subjective or that poor choices are less likely to be made by the user than in the selection of modes by the Bhattacharya method and in the choice of modes for the modal

progression analysis implemented in the LFSA package.

We feel that length-frequency analysis should not be used in the complete absence of information on growth and recruitment patterns or with very small data sets. Other important information includes data on migration and seasonal patterns in distribution, and such information should be used to guide sampling programs. Irregular recruitment both in terms of level and pattern may strongly affect the results. Clearly, length-frequency analysis can be a useful tool when used in conjunction with other methods. However, it seems unreasonable to expect such techniques to produce reliable information when the classical methods of fisheries fail or cannot be used. For example, traditionally, growth parameters have been estimated from age-length keys and mortalities derived from the age structure of the catch. In cases where the age-length key cannot be obtained, there is a temptation to obtain growth parameters at any cost using length-frequency analysis. If this is done, great care should be taken to ensure that a minimum amount of biological information exists. The use of length-frequency analysis as a "black box" where a length-frequency distribution goes in from one side and a whole set of biological parameters emerge does not seem correct. If as a first step, the data are plotted and there is no visual evidence of progressing modes, then even if biological information is available, length-frequency techniques should perhaps not be applied at all.

To have a more complete picture of the limitations and usefulness of length-frequency techniques, a much wider range of conditions must be tested. For example, the effect of variations in individual parameters particularly M and F, and in combinations of parameters must be tested. The effects of size class width on length-frequency analysis is also an area which should be investigated. It is the intention of the authors to continue this work in order to examine as wide a range of situations as possible.

ACKNOWLEDGMENTS

The authors would like to express their gratitude to Saul Saila for his guidance, advice, and support during the course of this work. The authors would also like to thank D. Pauly, P. Sparre, and an anonymous reviewer for their comments. This work was sponsored in part by USAID Grant No. DAN-4146-G-SS-5071-00 (Fisheries Stock Assessment CRSP).

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SPECIFYING A FUNCTIONAL FORM FOR THE INFLUENCE OF HATCHERY SMOLT RELEASE ON ADULT SALMON PRODUCTION

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ABSTRACT

The hypothesis of density independent marine survival of salmon has been tested extensively with conflicting results. Unduly restrictive functional form and data deficiency have been suggested as the major contributing factors to the mixed results. Focusing on the issue of functional form selection, this paper utilizes the extended Box-Cox flexible functional form which allows the data to determine the statistical relationship between smolts and adult production without a priori restrictions. The model is applied to Hokkaido chum salmon, *Oncorhynchus keta*, and Oregon coho salmon, *O. kisutch*. Empirical results suggest the existence of density dependence for both Hokkaido chum and Oregon coho salmon. Further, an increasing variability of adult production with respect to an increase in smolts is found for Hokkaido chum salmon but not for Oregon coho salmon.

Two issues pertaining to the relationship between the number of hatchery smolts released and the number of adult salmon returned have been investigated recently in the literature. First, the hypothesis of density independence in the relationship between salmon adults and smolts has been tested. The null hypothesis is a linear relationship between adults returned and smolts released, such that the additional adult salmon produced from an increase in smolts released is constant. The second issue is the relationship between the variability of adult production and the number of smolts released. If, in fact, increases in smolts increase the variability of adults produced, fishery management strategies can be improved by considering the trade-off between the mean and variance of adult salmon returned (Walters 1975; McCarl and Rettig 1983).

The empirical results of the test of density independence have been mixed. Nickelson (1986) provided an excellent discussion of previous results pertaining to the test of density independence for Oregon coho salmon. In short, this hypothesis for marine survival of Oregon coho salmon is rejected by McCarl and Rettig (1983) and Peterman and Routledge (1983), but accepted by Peterman (1981), Clark and McCarl (1983), and Nickelson (1986). In addition, biologists in the Oregon Department of Fish and Wildlife have examined several model specifications and manipulations in data sets and have drawn conflicting conclusions about density independence. This led McCarl and Rettig to suggest that conflicting conclusions are caused by the use of different functional form specifications and to suggest further that resolution of the issue of density independence in Oregon coho salmon requires more refined data. In the case of Hokkaido chum salmon, the null hypothesis of density independence fails to be rejected by McCarl and Rettig.

Regarding the estimation of the variability of adult salmon production, Peterman (1981) pointed out the importance of functional form specification and argued for the use of the multiplicative-error model rather than an additive-error model. McCarl and Rettig (1983) demonstrated that the specification of a multiplicative-error model imposes unwarranted restrictions on the estimation of the variability in adult production. McCarl and Rettig utilized the specification developed by Just and Pope (1978, 1979). As a result, the variability in adult salmon production is estimated and conflicting conclusions of the test of density independence emerged.

It is apparent that functional form specification is critical in the test of density independence and the estimation of variability in adult production. The purpose of this paper is to reexamine these two issues by using the extended Box-Cox flexible functional form. Both Hokkaido chum salmon, *Oncorhynchus keta*, and Oregon coho salmon, *O. kisutch*, data are used in this study.

The next section of the paper discusses the importance of the functional form specification and demonstrates the superior flexibility of the Box-Cox

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Manuscript accepted July 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

functional form compared with the Just-Pope specification used by McCarl and Rettig (1983). The empirical results of the Box-Cox functional form are then discussed and compared with those of McCarl and Rettig.

METHODS

Previous findings of Peterman (1978, 1981) indicate the importance of the assumption made regarding error term in testing the hypothesis of density independence. In the process of examining the effect of the number of released smolts on the production of adults and its variability, Peterman (1981) employed two alternative (additive-error and multiplicative-error) model specifications of the error term:

$$A_1 = C_1 S^{k_1} + V_1 \quad \text{...Additive-error model} \quad (1)$$

$$A_2 = C_2 S^{k_2} \exp(V_2) \quad \text{...Multiplicative-error model} \quad (2)$$

where A_i = adult production of salmon using specification i,
S = number of smolts,
C_i = survival rate parameter in model i,
k_i = density dependence parameter in model i,
V_i = error term for model i.

By applying these two models to several sets of salmon data, Peterman (1981) concluded that the multiplicative-error model appears to generate better statistical results than its counter model. In addition, the results of the multiplicative-error model suggest that an increase in the number of smolts will increase the variation in total adult returns. Because the variability in adult production is not only influenced by the number of smolts but also other factors affecting the survival of smolts such as the body size of released smolts, Peterman (1981) suggested that model (2) should be modified by including more explanatory variables. By following Peterman's suggestion a third model can be specified with the additional variable body size, B:

$$A_3 = C_3 S^{k_3} B^{d_3} \exp(V_3). \quad (3)$$

The mean and variance of adult production for this model can be expressed as

$$E(A_3) = C_3 S^{k_3} B^{d_3} E(\exp(V_3))$$

$$\mathrm{Var}(A_3) = (C_3 S^{k_3} B^{d_3})^2 \mathrm{Var}(\exp(V_3)).$$

The instantaneous rates of change in mean and variance of adult production with respect to smolt body size can be expressed as

$$\partial E(A_3)/\partial B = d_3 E(A_3)/B$$

$$\partial \mathrm{Var}(A_3)/\partial B = 2(\mathrm{Var}(A_3)/E(A_3))\,\partial E(A_3)/\partial B.$$

If body size of smolts is enlarged, one would expect higher yields, $\partial E(A_3)/\partial B > 0$. Since both mean and variance are positive, the above model imposes a restriction that the smolt body size has a positive effect on variability, $\partial \mathrm{Var}(A_3)/\partial B > 0$. This restriction is unwarranted because of lacking theoretical support; rather the effect (positive, negative, or zero) of body size on variability of adult return should be tested empirically. For this reason, McCarl and Rettig (1983) adopt a model developed by Just and Pope (1978, 1979) which can be expressed as

$$A_4 = C_4 S^{k_4} B^{d_4} + C_5 S^{k_5} B^{d_5} \exp(V_4)$$

$$= f(S,B) + h^{1/2}(S,B) \exp(V_4) \quad (4)$$

where $h^{1/2}(S,B)$ is a component of the standard deviation of adult production as shown below.

The mean and variance of adult production for this model can be expressed as

$$E(A_4) = C_4 S^{k_4} B^{d_4} + C_5 S^{k_5} B^{d_5} E(\exp(V_4))$$

$$\mathrm{Var}(A_4) = (C_5 S^{k_5} B^{d_5})^2 \mathrm{Var}[\exp(V_4)].$$

Because the signs of d_4 and d_5 are to be determined in the estimation, the advantage of model (4) over model (3) is that it allows for body size to have a positive effect on mean return and unknown (positive, negative, or zero) effect on the variability of adult production.

There are problems inherent in model (4), however, the first being that this specification produces a constant percentage change (k_4) in adult production when the number of smolts released changes by 1%, a constant output elasticity, ε_{as}. Output elasticity is an economic term which is widely used in measuring the relationship between input (smolt release) and output (adult production) and has the advantage of being unit free. An output elasticity of 1.0 means that an increase in smolt release by 1% will result in the same percentage increase in

adult production, implying density independence. When the hypothesis of density independence is rejected, output elasticity is less than 1.0. Therefore, there is an one-to-one correspondence between the hypothesis of density independence and the value of output elasticity. The purpose of using the concept of output elasticity here is to facilitate the discussion of the restriction inherent in model (4).

There is no theoretical support for imposing the restriction of constant output elasticity, rather it should be treated as a hypothesis to be tested. More important, body size (B) is likely to have a positive effect on the output elasticity, i.e., $\partial \varepsilon_{as}/\partial B > 0$. In other words, when body size of smolts is enlarged, the improved ability of enduring unfavorable environmental conditions should increase the incremental return rate of adult salmon. But, a constant output elasticity implies that body size and the output elasticity are independent.

The comparison between model (3) and model (4) centers around the role of body size in the variability of adult production. However, data on body size is unavailable so that the comparison becomes empirically irrelevant. Consequently, the difference between these two models, in essence, rests on model specification. It should also be pointed out that the estimate of $h^{1/2}(S,B)$ is influenced by the functional form of $f(S,B)$ and vice versa, because $h^{1/2}(S,B)$ is the heteroscedastic error term to be handled by the weighted least squares method. It is, therefore, important to select a more general functional form for the mean and variance of adult production in testing the hypothesis of density independence and in estimating the variability in adult production.

The Box-Cox flexible functional form developed by Box and Cox (1964) and extended by Zarembka (1974) has been a popular tool for both discriminating among alternative functional forms and providing added flexible form in model specification (Moschini and Meilke 1984). The extended Box-Cox functional form for relating adult salmon production to smolts and other explanatory variables X (such as upwelling) can be expressed as

$$A^{(\lambda)} = \alpha_0 + \alpha_1 S^{(\mu)} + \alpha_2 X^{(\theta)} + e \qquad (5)$$

where $A^{(\lambda)} = \begin{cases} (A^{\lambda} - 1)/\lambda & \text{for } \lambda \neq 0 \\ \ln A & \text{for } \lambda = 0 \end{cases}$

$$S^{(\mu)} = \begin{cases} (S^{(\mu)} - 1)/\mu & \text{for } \mu \neq 0 \\ \ln S & \text{for } \mu = 0 \end{cases}$$

$$X^{(\theta)} = \begin{cases} (X\theta - 1)/\theta & \text{for } \theta \neq 0 \\ \ln X & \text{for } \theta = 0 \end{cases}$$

$$e \sim \text{NID}(0, \sigma_1^2).$$

Model (5) includes the linear ($\lambda = \mu = \theta = 1$), multiplicative-error or log-log ($\lambda = \mu = \theta = 0$), and log-linear ($\lambda = 0$, $\mu = \theta = 1$) functional forms as special cases. Therefore, models (3) and (4) are special cases of model (5), which allows both nonconstant output elasticity and nonzero effect of X on the output elasticity.[3]

When the variability of adult salmon production is affected by the values of its explanatory variables, the error term has nonconstant variance, i.e., heteroscedasticity. Zarembka (1974) demonstrated that while the Box-Cox model is fairly robust to departures from normality, it is sensitive to heteroscedasticity. Failure to correct for this problem can generate misleading results (Lahiri and Egy 1981). When heteroscedasticity is present, we can also specify a Box-Cox functional form for the variance of the error term in model (5) as the following:

$$e \sim NID(0, h(S,X)\,\sigma_2^2) \qquad (6)$$

where $h(S,X) = \beta_1 S^{(\tau)} + \beta_3 X^{(\xi)}$.

The parameters, α_i, β_i, λ, μ, θ, τ, and ξ can be estimated by maximum-likelihood algorithms (see Appendix for a discussion of the log-likelihood function and estimation methods). The hypothesis of density independence can be tested by estimating the model with the restriction that $\lambda = \mu = 1$ against the unrestricted model.

[3]The superior flexibility of model (5) compared with models (3) and (4) is an important consideration in testing the hypothesis of density independence in light of the following remarks on the comparison of models (1) and (2) in Peterman (1981, p. 1117):

> "This is not to say that model 2 is the 'true' form of natural variability, because there are numerous other models that were not tested here (many of these alternatives cannot be tested in practice). . . ."

We also cannot claim that the extended Box-Cox functional form can produce the "best" or "true" functional form. There exist other flexible functional forms, such as Fourier (Gallant 1984), and the literature is silent in the comparison of these flexible functional forms.

Even though the Box-Cox functional form was first proposed in 1964, its application and investigation of its statistical properties have not received much attention until recently. Therefore, there are numerous aspects of transformations that merit further study (Box and Cox 1982). Lacking software support also makes its application difficult. Nevertheless, the superior flexibility of the Box-Cox functional form compared with other functional forms used traditionally is evident and its application should be encouraged.

RESULTS

In order to test the hypothesis of density independence for salmon utilizing the extended Box-Cox flexible functional form, the two data sets analyzed by McCarl and Rettig (1983) were also used here. The first data set contains total Hokkaido hatchery chum salmon fry releases and brood year adult returns for the years 1950 through 1969 (Moberly and Lium 1977). The second data set pertains to Oregon coho salmon for the years 1960 through 1980 (Oregon Department of Fish and Wildlife 1982). This latter data set was also analyzed by Clark and McCarl.

Hokkaido Chum Salmon Results

Due to the lack of data on body size and other factors affecting the survival rate of fry, adult production (in thousands) is estimated with the single explanatory variable, number of fry released (in millions). As explained in the Appendix, the dependent variable is divided by its geometric mean of 3,332,440. The iterated weighted least squares method produces the following maximum log-likelihood results with the t-statistics given in parentheses below the coefficients:

$$A^{(-0.4)} = \underset{(-4.07)}{-1{,}254} \; \underset{(4.07)}{-1{,}756.3S^{(-1.4)}} \qquad (7)$$

$R^2 = 0.48$, Durbin-Watson = 1.5, Log-likelihood = -7.89.

The weight used to remove heteroscedasticity is $S^{(1.06)} = (S^{1.06} - 1)/1.06$. This implies that as the number of fry is increased by 1%, the standard deviation of the adult production increases by 1.06%, which is much smaller than the 2.5% reported by McCarl and Rettig (1983).

The above results suggest that the output elasticity[4] of fry is $1{,}756.3A^{0.4}S^{-1.4}$. When evaluated at the mean values of A and S (which are 1.1278 and 288.36, respectively), a percentage increase in the number of fry increases the adult production by 0.66%, implying density dependence. In addition, this output elasticity is a decreasing function of fry releases. In contrast to these results, McCarl and Rettig (1983) reported a constant output elasticity of 1.09 which was not found to be statistically different from 1.0, supporting density independence.

The hypothesis of density independence was formally tested by estimating the linear relationship between A and S (i.e., the power transformations for A and S are restricted to be one) by using the weighted least squares method (S was treated as the weight) with the following results:

$$A = \underset{(0.6)}{0.18} + \underset{(2.84)}{0.0034S} \qquad (8)$$

$R^2 = 0.31$, Durbin-Watson = 1.04, Log-likelihood = -12.56.

The weighted least squares method produces a Durbin-Watson value of 1.04 which is below the lower limit of its critical value, suggesting the possible existence of autocorrelation. However, the Durbin-Watson value is well known to be below the lower limit (or above the upper limit) which could be the cause by model misspecification or autocorrelated error terms. Because the use of improper functional form is a model misspecification, the extended Box-Cox functional form needs to be explored before assuming the existence of an autocorrelation problem in light of low (or high) Durbin-Watson statistics. The extended Box-Cox results have a Durbin-Watson statistic of 1.50 (implying no autocorrelation), and hence, it is concluded that the low Durbin-Watson value in Equation (8) is a result of incorrect functional form. Since the Durbin-Watson statistic is for detecting first-order autocorrelation, the least squares procedure described in Pagan (1974) was applied to test higher-order autocorrelation. It is concluded that the Box-Cox results are free from autocorrelation problems, first or higher orders.

The hypothesis of density independence can be tested by comparing the log-likelihood values of Equations (7) and (8). The test statistic of twice the difference between the log-likelihood functions under the two specifications follows a chi-square distribution with the number of degrees of freedom equal to the number of restrictions (Theil 1971). This test procedure is similar to the Akaike Information Criterion (Akaike 1974) and has the advantage of testing the significance of the difference between the log-likelihood functions of different model specifications. It is concluded that the density-indepen-

[4]Equation (7) can be written as

$(A^{-0.4} - 1)/(-0.4) = -1254 + 1756.3(S^{-1.4} - 1)/(-1.4)$, or $A^{-0.4} = 0.8 + 501.8S^{-1.4}$.

Output elasticity $\varepsilon_{as} = (\%\Delta A)/(\%\Delta S) = dA/dS)\ (S/A) = 1{,}756.3S^{-1.4}A^{0.4}$ $d\varepsilon_{as}/dS = -2{,}458.8S^{-2.4}A^{0.4} < 0$.

dence hypothesis can be rejected at a 1% level with a critical value of 9.21 at 2 degrees of freedom.

For comparison purposes, the Hokkaido chum salmon data was used to fit the multiplicative-error model (model (2)) by applying the weighted least squares method with the following results:

$$\ln(A) = \underset{(2.06)}{-3.27} + \underset{(2.06)}{0.583}\ln(S) \qquad (9)$$

$R^2 = 0.19$, Durbin-Watson = 1.15, Log-likelihood = −11.22.

By comparing the values of the log-likelihood function of Equations (7) and (9), it can be concluded that the multiplicative-error model can be rejected a 5% significance level. Even though the multiplicative-error model produces a bigger log-likelihood value than the linear model, the difference between these two log-likelihood values is not statistically signifi-

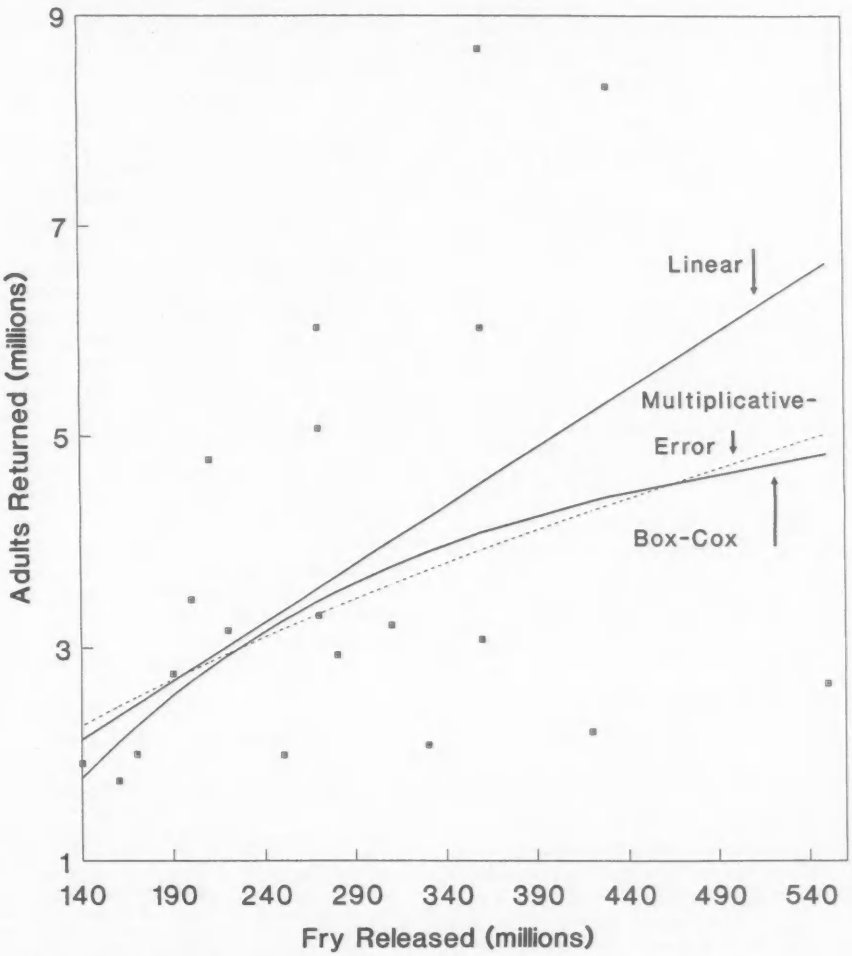

FIGURE 1.—Plot of Hokkaido chum salmon data and estimated relationships: 1950–1969. Dots are actual observations, linear model is Equation (8), multiplicative-error model is Equation (9), and Box-Cox model is Equation (7).

cant. Figure 1 shows the data set with estimated relationships, Equations (7)–(9), superimposed. It is evident that the Box-Cox specification produces a relationship of much bigger curvature and better fit than the multiplicative-error specification.

Oregon Coho Salmon Results

McCarl and Rettig (1983) suggested that aggregated (wild and hatchery) adult coho salmon production (in thousands) is affected by smolt releases (in millions), S, and upwelling index, U. The flexible functional form for Oregon coho salmon can be expressed as Equation (5). The model was estimated by iterated ordinary least squares with the following maximum log-likelihood results:

$$A^{(-0.6)} = \underset{(-1.17)}{-50.08} + \underset{(1.08)}{93.71}S^{(-2.0)} + \underset{(3.37)}{0.59}U^{(0.0)} \quad (10)$$

$R^2 = 0.51$, Durbin-Watson = 2.07, Log-likelihood = −1.66.

To detect any violations of the assumption regarding the homoscedastic error term, a series of tests were conducted by running regressions of squared residuals ($\hat{e}^2$) or logs of ($\hat{e}^2$) on the predicted values of A or the explanatory variables S and U. The regression of $\hat{e}^2$ on all explanatory variables is known as the Breusch-Pagan-Godfrey test and the regression of $\log(\hat{e}^2)$ on all explanatory variables are known as the Harvey test (White 1987). Five tests were conducted using the chi-square distribution, and the assumption of homoscedastic error fails to be rejected at a 5% significance level. The same conclusion is reached when model (2) was fitted by Peterman (1981). The Box-Cox results are also found to be free from autocorrelation problems, first or higher orders.

Empirical results as summarized in Equation (10) indicate that the number of smolt released contributes positively to adult production at a 15% significance level. Upwelling also positively affects adult production at a 1% significance level. The Box-Cox results produce a nonlinear relationship between adult production and smolt release and an output elasticity of less than one, suggesting that the null hypothesis should be rejected. To formally test the hypothesis of density independence, the power transformations for A and S are restricted to be 1.0 and the Box-Cox functional form is re-estimated with the following results:

$$A = \underset{(-1.2)}{-0.58} + \underset{(0.1)}{0.00065}S + \underset{(3.6)}{0.084}U^{(0.39)} \quad (11)$$

$R^2 = 0.41$, Durbin-Watson = 2.09, Log-likelihood = −6.54.

By comparing the values of the log-likelihood functions for Equations (10) and (11) and following a chi-square test with 2 degrees of freedom, it is concluded that the hypothesis of density independence for Oregon coho salmon can be rejected. The same conclusion was reached by Peterman and Routledge (1983) and McCarl and Rettig (1983).

CONCLUSION

The findings of testing the hypothesis of density-independent marine survival for salmon and of the effect of the number of smolts released on the variability of adult production have important implications for fishery managers as noted in the literature. If the hypothesis of density independence fails to be rejected, there is no technical maximum[5] for the adult production from releasing smolts. A technical maximum of adult production exists when the number of smolts has a positive and decreasing effect on adult production. If the variability of adult production is positively affected by the number of smolts, it will be useful for fishery managers and the fishing industry to know the form of variability to evaluate the effectiveness of salmon hatchery operations. Further, fishery managers can improve management strategies by considering the trade-off between the mean and variance of adult production. The hypothesis of density independence has been tested extensively for different sets of data with conflicting results. Functional form selection and data deficiency have been suggested as the causes of conflicting findings.

Results of this study confirm that functional form selection is critical in testing the hypothesis of density independence and estimating the form of the variability of adult production. By using the extended Box-Cox functional form, it is concluded that there exists a density-dependent relationship be-

[5]A "technical maximum" refers to the maximum adult production in physical terms. This may not be an appropriate objective for fishery managers to achieve, because the release of smolts at technical maxima may not generate maximum benefits to the fishing industry. Maximization of the return to hatchery operations appears to be a more suitable objective of a single-attribute model to be accomplished without considering the risk factor.

tween the adult production and the number of chum salmon fry released in Hokkaido. Also, as the number of fry increases, the variability in adult production increases as well. The results reported by McCarl and Rettig (1983), using the Just-Pope specification (a special case of extended Box-Cox), conclude that the hypothesis of density independence fails to be rejected and the effect of the number of fry on the variability of adult production is more than twice that of this study. The Box-Cox results of aggregated Oregon coho salmon also indicate density dependence, and the same conclusion is also reached by McCarl and Rettig (1983) and Peterman and Routledge (1983). Because Nickelson (1986) reached a different conclusion using disaggregated data, the use of the extended Box-Cox specification to analyze disaggregated data for Oregon coho salmon is, therefore, recommended by the authors as a possible research need. However, partitioning the data set according to high and low upwelling, for example, will lead to the problem of insufficient degrees of freedom, as pointed out by an anonymous reviewer. This can be overcome only after a sufficient number of years of data collection have transpired. Finally, data reliability needs to be secured before the selection of functional form can improve our understanding of this issue.

ACKNOWLEDGMENTS

This work is the result of research sponsored by the Alaska Sea Grant College Program, cooperatively supported by the U.S. Department of Commerce, NOAA Office of Sea Grant and Extra-Mural Program, under grant number NA86AA-D-SG041, project number R/14-09; and by the University of Idaho with funds appropriated by the state.

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APPENDIX

Because the estimation of the extended Box-Cox functional form is carried out by maximum likelihood procedures, the log-likelihood function for the extended Box-Cox functional form and estimation methods are briefly presented in this appendix.

Under the assumptions that S and B are nonstochastic and the error term is normally and independently distributed with zero mean and constant variance, σ_1^2, the log-likelihood function of model (5) can be expressed following Spitzer (1982):

$$L(\alpha, \lambda, \mu, \theta, \sigma_1^2) = -T/2(\ln 2\pi + \ln \sigma_1^2) - (2\sigma_1^2)^{-1}(e'e) + (\lambda - 1)\Sigma \ln A \tag{12}$$

where T is the number of observations. To reduce the dimension of the estimation problem, the parameter σ_1^2 can be eliminated from Equation (12) to derive the concentrated log-likelihood function as follows:

$$L(\alpha, \lambda, \mu, \theta) = -T/2(\ln 2\pi + \ln \hat{\sigma}_1^2) + (\lambda - 1)\Sigma \ln A$$

where $\hat{\sigma}_1^2 = (1/T)\hat{e}'\hat{e}$.

When heteroscedasticity is present, the concentrated log-likelihood function for model (5) and the error term expressed in model (6) can be expressed as

$$L(\alpha, \lambda, \mu, \theta) = -T/2(\ln 2\pi + \ln \hat{\sigma}_2^2 + 1)$$

$$- \Sigma \ln (\beta_1 + \beta_2 S^{(\tau)} + \beta_3 B^{(\zeta)}) + (\lambda - 1)\Sigma \ln A \tag{14}$$

where $\hat{\sigma}'^2_2 = (1/T)\hat{e}'V^{-1}\hat{e}$ and V is a $n \times n$ matrix (n is the number of observations) in which off-diagonal elements are zeros and diagonal elements are $\beta_1 + \beta_2 S^{(\tau)} + \beta_3 B^{(\zeta)}$.

The maximum log-likelihood parameter estimates for ($\alpha, \lambda, \mu, \theta$, and β) can be obtained by nonlinear least squares methods or iterated ordinary (weighted) least squares procedures. Seaks and Layson (1983) provide an example of the iterated ordinary (weighted) least squares method using the Time Series Processor (TSP) computer package for estimating Box-Cox flexible functional form with standard econometric problems; i.e., heteroscedasticity and autocorrelation.

As Spitzer (1984) pointed out, the ordinary least squares method underestimates the variance of the error term while the first derivative only gradient estimation methods (e.g., Marquardt) overestimate the variance. In order to compress the range of under- and overestimation of the error variance, Spitzer suggested that the dependent variable be divided by its geometric mean. This scaling process will then eliminate the last term in the concentrated log likelihood function in Equations (12)–(14).

AGE, MORPHOLOGY, DEVELOPMENTAL BIOLOGY, AND BIOCHEMICAL GENETIC VARIATION OF YUKON RIVER FALL CHUM SALMON, *ONCORHYNCHUS KETA*, AND COMPARISONS WITH BRITISH COLUMBIA POPULATIONS

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ABSTRACT

Fall chum salmon, *Oncorhynchus keta*, populations spawning in the Yukon River drainage were surveyed for variation in age, size and shape at maturity, developmental biology, and biochemical genetics. Yukon River fall chum salmon matured at older ages and smaller sizes than chum salmon in British Columbia. They also had proportionately smaller heads, thinner caudal peduncles, and smaller fins than British Columbia chum salmon, perhaps illustrating morphometric adaptation to long distance freshwater migration. Yukon River chum salmon were less fecund and had smaller eggs than those in British Columbia, and they also tended to have faster development to alevin hatching and fry emergence than most British Columbia populations. Maximum alevin and fry size of Yukon River salmon occur at lower water temperatures during development than for most British Columbia populations, possibly indicating a developmental adaptation to low winter water temperatures. Genetic differentiation among chum salmon populations in the Yukon River drainage was observed.

The Yukon River is a major North American river, originating in British Columbia and flowing over 3,200 km through the Yukon Territory and Alaska to the Bering Sea, and draining an area of approximately 860,000 km^2. Five species of Pacific salmon (*Oncorhynchus*) occur in the Yukon River (Gilbert 1922), but chinook, *O. tshawytscha*, and chum salmon, *O. keta*, are the most abundant and are exploited in commercial and subsistence fisheries (McBride et al. 1983). Chum salmon in the Yukon River are characterized by distinct seasonal races (Gilbert 1922). The early-maturing or "summer" chum salmon return to the Yukon River between early June and mid-July and spawn in the lower 800 km of the drainage (Buklis 1981). Later-maturing or "fall" chum salmon enter the Yukon River from mid-July through late August and spawn in the up-river portions of the drainage, migrating as far as 2,800 km upstream (Milligan et al. 1986). Fall chum salmon are also larger than summer chum salmon (Buklis 1981; Buklis and Barton 1984), and generally have higher fecundity and younger age compositions than summer chum salmon (Sano 1966).

Chum salmon generally spawn in rivers only a short distance from salt water (≤200 km), a trait very different from the long distance freshwater migrations of Yukon River fall chum salmon. Yukon River fall chum salmon are noted for their high oil content upon entering the river (Gilbert 1922), an adaptation necessary to provide sufficient energy reserves for the freshwater migration, as in Amur River chum salmon in the Soviet Union (Nikol'skii 1961). Adaptations in other biological characters may reflect the environmental conditions experienced by Yukon River fall chum salmon. Thus we examined the variation in life history traits of Yukon River fall chum salmon, and compared this variation to that found in chum salmon in British Columbia.

In 1984, we began a survey of variation in biological characters of fall chum salmon in the Yukon River. Regional biochemical genetic variation had previously been reported for chum salmon in British Columbia (Beacham et al. 1987), and we investigated the biochemical genetic differentiation of Yukon River fall chum salmon. We had previously examined the adaptive nature of the variation in some morphometric and life history traits of chum salmon in British Columbia (Beacham and Murray 1987) and used this for comparison for Yukon River fall chum salmon.

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Manuscript accepted July 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

METHODS AND MATERIALS

Age and Morphology

Chum salmon were collected with gill nets. After capture in 1984, postorbital-hypural length (Vladykov 1962), caudal peduncle depth, and length of the base and height of the anal and dorsal fins were all recorded on the left side in the field to the nearest millimeter. The number of gill rakers on the left anterior arch was recorded, as well as the number of branchiostegal rays on the left side. Five scales and two otoliths were collected from each individual for age determination, and the sex of an individual was confirmed by internal inspection. When the age of an individual estimated from scales and from otoliths disagreed, the age determined from scales was assigned. In 1985, only postorbital-hypural length and sex were recorded for individuals, and only scales were collected for age determination.

Population differences and sexual dimorphism in the meristic characters were examined by two-way analysis of variance, with population and sex as the indices. Population is used in the manner as described by Ricker (1972), as a group of fish spawning in a particular river at a particular season, and there is no substantial interbreeding with another group spawning in a different river. Morphometric measurements of both males and females were standardized to a postorbital-hypural length of 520 mm by the method outlined by Beacham and Murray (1983):

$$M_t = M_o \left(\frac{\bar{L}}{L_o} \right)^b$$

where M_t = size of standardized morphometric character,
M_o = observed character size,
$\bar{L}$ = length that characters are standardized to (520 mm),
l_o = observed postorbital-hypural length, and b is the regression coefficient of $\log_e M_o$ on $\log_e L_o$ (stocks and sexes separate).

Two-way analysis of variance was again used to examine population differences and sexual dimorphism in the morphometric characters.

Developmental Biology

We estimated fecundity of Yukon River chum salmon by collecting and freezing both ovaries from 14 females in the Dawson City commercial fishery in 1985 (we also collected length and scales); we subsequently thawed both ovaries and made total egg counts for each female. The methodology of the survey of developmental biology was similar to that outlined by Beacham and Murray (1987). Gametes were collected from five male and five female Kluane River chum salmon on 17 October 1985. The gametes were then shipped to the laboratory on ice, the eggs fertilized at 8°C, and then subsequently reared in controlled water temperatures of 4°, 8°, and 12°C in vertical stack incubators. Five full-sib families were obtained from the crosses, with each family replicated in each incubator. Water temperatures were recorded daily, and mean temperatures in the incubators during the study were 4.1° (SD = 0.29), 8.0° (SD = 0.44), and 12°C (SD = 0.40), respectively.

Egg diameter (millimeters) and weight (milligrams) for each female were determined from 30 water-hardened eggs preserved for at least 3 months in 10% formalin. During incubation, dead eggs were removed from each family, stored in Stockard's solution, and later inspected to remove unfertilized eggs. Egg survival rates were then calculated based upon the number of eggs initially fertilized. Once hatching began in each family, we recorded the number of newly hatched alevins daily, and within 1 day of 50% hatching we anesthetized and preserved 30 per family in 10% formalin for subsequent determination of alevin length and weight. Fork length was recorded to the nearest 0.1 mm, total weight recorded to the nearest milligram, the yolk separated from the rest of the body and weighed (milligrams), and then tissue weight (milligrams) determined by subtraction. Dead alevins were also removed and counted in order to determine alevin survival rates. The timing of fry emergence (swim-up) for each family was determined by placing the alevins in an emergence trap modified from Mason (1976), where the alevins were classified as newly emergent fry only when they became neutrally buoyant and positively phototactic. When 50% of the fry from a particular family had emerged, all of the family remaining in the incubator was anesthetized and then preserved in 10% formalin, and 30 fry were randomly drawn from the preserved samples and fry length and weight determined as for alevins.

Variation in egg size was analyzed with a one-way (female was the index) analysis of variance. Variation in survival rates was analyzed by first determining survival rates for each group as proportions and then transforming them to radians with the arcsine

square root transformation to normalize the data. We then used an analysis of variance model:

$$Y_{ijkl} = \mu + T_i + F_j + TF_{ij} + R_{ijk} + e_{ijkl}$$

where Y_{ijkl} = transformed survival rate,
μ = overall mean,
T_i = fixed effect of temperature (i = 1–3),
F_j = random effect of family (j = 1–5),
TF_{ij} = random interaction between temperature and family,
R_{ijk} = random effect of replicate (k = 1–2), and
e_{ijkl} = error term for lth observation in subgroup ijk.

Variation in alevin and fry size characters was analyzed with the same model. Satterthwaite's (1946) approximation was necessary to calculate an appropriate mean square to test the effect of family.

Biochemical Genetics

Biochemical genetic sampling began on Canadian populations in 1984 and was expanded in 1985 to include United States populations (Fig. 1). Methodology of sample collection has been outlined by Beacham et al. (1985). Summarized briefly, heart, liver, and muscle samples were collected from adult chum salmon, frozen, and stored at −20°C for later electrophoretic analysis by a consultant. We verified the scoring of all gels from a complete photographic record. Horizontal starch gel electrophoresis, described by Utter et al. (1974), was used to detect protein variation. The loci and buffer systems used

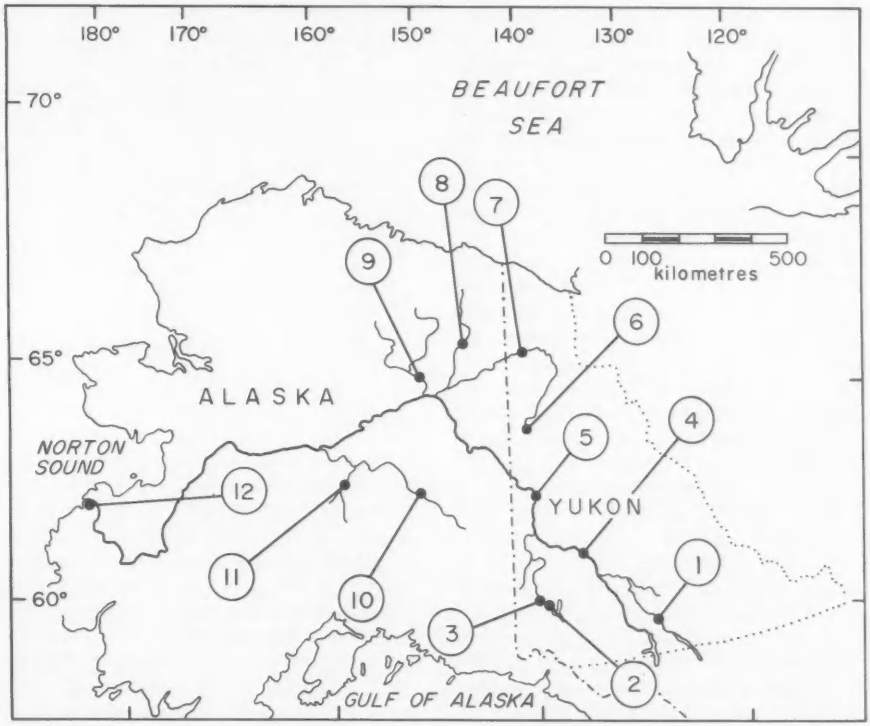

FIGURE 1.—Locations in Yukon River drainage where chum salmon were sampled during 1984–1986. Listed in ascending order are (1) Teslin River, (2) Kluane River, (3) Koidern River, (4) Yukon River at Minto, (5) Dawson City, (6) Fishing Branch River, (7) Porcupine River at Old Crow, (8) Sheenjek River, (9) Chandalar River, (10) Delta River, (11) Toklat River, (12) Yukon River at Emmonak.

are outlined in Beacham et al. (1985). *Lgg* was renamed as Tapep and was scored as a four-allele locus (L. Seeb[2]) (although only three were present in the stocks we surveyed) on both a Tris-boric acid-EDTA buffer described by Markert and Faulhaber (1965) and an amine citrate buffer described by Clayton and Tretiak (1972). *Me* was renamed as *MdhP*, *6-Pg* as *Pgdh*, *Pmi* as *Mpi*, and *Agp* as *G3pdh*.

We determined allelic frequencies for each locus by summing the numbers of each allele and dividing by the total number of alleles counted. Genotypic frequencies at each polymorphic locus in each population were tested for departures from Hardy-Weinberg equilibrium by chi-square. We used the log-likelihood ratio statistic (*G*-test) (Sokal and Rohlf 1969) to test equality of allelic frequencies between countries, among populations within countries, and between years for samples taken from the same population. An approximate *F*-ratio (*G*-statistic summed over all loci/degrees of freedom) was used to test the relative magnitude of the sources of variation. We calculated genetic distance among populations using Nei's (1978) statistic and the 7 loci indicated in Table 7 and constructed a denogram from the matrix of the distances using the unweighted pair group mean method of Sneath and Sokal (1973).

RESULTS

Age and Morphology

Age of Maturity

The dominant age of maturity for fall chum salmon returning to Canadian rivers during 1984 and 1985 was four years, with age 3 and age 5 chum salmon each comprising less than 15% of the total return (Table 1). The proportion of chum salmon returning at three or five years of age varied annually within a population, possibly reflecting different production from the respective brood years. Yukon River chum salmon matured at a significantly older age than chum salmon in British Columbia ($X_2^2 = 193.9$, $P < 0.01$), but four years was the dominant age of maturity in both areas. Of 227 chum salmon sampled in 1984 from which age could be determined from both otoliths and scales, the same age was recorded in 184 (83%) of the cases. For the 43 other fish, the age estimated from scales was one year older than that estimated from otoliths in 22 cases, whereas in the remaining 21 fish, the age estimated from otoliths was either one year (19 cases) or two years (2 cases) older than that estimated from scales. In 1984, age could not be determined from 16% (48 fish) of the scales collected and 9% (26 fish) of the otoliths collected. In 1985, age could not be determined from 18% (124 fish) of the scales examined due to scale resorption. Age of maturity was more likely to be determined from otoliths than from scales.

TABLE 1.—Percentage of chum salmon returning at ages 3–5 years and mean age of return for Yukon River populations sampled on the spawning grounds during 1984–85. The mean for British Columbia chum salmon was derived from Beacham and Murray (1987).

Population	Year	N	Age (yr) 3	4	5	Mean age (yr)
Yukon River						
Kluane	1984	100	16.0	78.0	6.0	3.90
	1985	96	29.2	70.8	0.0	3.71
Total		196	22.4	74.5	3.1	3.81
Minto	1984	100	13.0	69.0	18.0	4.05
	1985	99	25.3	72.7	2.0	3.77
Total		199	19.1	70.9	10.0	3.91
Fishing Branch	1984	100	14.0	82.0	4.0	3.90
	1985	77	1.3	72.7	26.0	4.25
Total		177	8.5	78.0	13.5	4.05
Porcupine	1985	67	1.5	85.1	13.4	4.12
Teslin	1985	64	0.0	56.3	43.7	4.44
Koidern	1985	81	0.0	74.1	25.9	4.26
Total						
Mean		784	12.5	73.7	13.8	4.01
British Columbia						
Total						
Mean		11,749	32.4	62.1	5.5	3.73

Meristics

No sexual dimorphism was observed in the number of gill rakers or branchiostegal rays ($P > 0.05$). No population differences in gill raker number were observed ($P > 0.05$), but significant differences among populations were observed in branchiostegal ray number ($F_{2,297} = 4.36$, $P < 0.05$). The population with the greatest number of gill rakers (Fishing Branch) also had the greatest number of branchiostegal rays (Table 2). Yukon River chum salmon had more gill rakers and branchiostegal rays than the average British Columbia chum salmon.

Morphometry

Yukon River male chum salmon were longer than

[2]University of Idaho, Moscow, ID 83843, pers. commun. December 1985.

females at all ages examined ($P < 0.05$) (Table 3). Although there could be significant variation in mean length-at-age among populations ($P < 0.05$), Yukon River chum salmon were substantially smaller than chum salmon of the same age spawning in British Columbia ($P < 0.05$). Size differences between Yukon River and British Columbia chum salmon increase with age, with age 3 Yukon River males 94% of the length of age 3 British Columbia males, but age 5 Yukon River males are 86% of the length of their British Columbia counterparts. Similar results were also observed for females.

We examined whether there was any differentiation of selected morphometric characters with respect to sexual dimorphism or distance of freshwater migration. With the morphometric measurements of both males and females standardized to a postorbital-hypural length of 520 mm, males had longer postorbital head lengths, thicker caudal peduncles, longer base length of the dorsal fin, and longer dorsal and anal fins (all $P < 0.05$) (Table 4). No sexual dimorphism in base length of the anal fin was observed. Significant population differences in the relative sizes of the morphometric characters were also observed, with the Kluane River population having the relatively smallest characters, and the Fishing Branch River population having the proportionately largest characters.

Substantial differences exist in length of freshwater migration between Yukon River fall chum salmon and chum salmon in British Columbia. The relative sizes of the morphometric characters examined are all smaller for Yukon River chum salmon than for chum salmon in British Columbia (Table 4), perhaps illustrating morphometric adaptation of Yukon River chum salmon to the long freshwater migration.

TABLE 2.—Mean number of gill rakers on left anterior gill arch and mean number of branchiostegal rays on left side for Yukon River fall chum salmon sampled during 1984. Standard error of mean is in parentheses. One hundred fish were sampled per population. Data for 9,206 British Columbia chum salmon are from Beacham and Murray (1987).

Population	Gill rakers	Branchiostegal rays
Yukon River		
Kluane	22.88 (0.10)	13.72 (0.07)
Minto	22.90 (0.09)	13.58 (0.08)
Fishing Branch	23.13 (0.09)	13.89 (0.07)
Mean	22.97 (0.05)	13.73 (0.04)
British Columbia		
Mean	22.62 (0.01)	13.42 (0.01)

Developmental Biology

Fecundity and Egg Size

The fecundity-length relationship for 14 female chum salmon is described by

$$F = 0.100\ L^{1.60}$$

where F = number of eggs and L is postorbital-hypural length (mm). Mean fecundity of age 4 females was 2,271 eggs (SD = 208, n = 7), and that of age 5 females was 2,451 eggs (SD = 106, n = 3).

Mean egg weight of the five Kluane River females used in the study of developmental biology ranged from 145 mg (SD = 6 mg) to 210 mg (SD = 5 mg). Mean diameters ranged from 6.66 mm (SD = 0.21 mm) to 7.25 mm (SD = 0.18 mm). Mean egg size of Yukon River chum salmon is substantially smaller than the mean weight of 290 mg and mean diameter of 8.39 mm for egg size of chum salmon in

TABLE 3.—Mean postorbital-hypural length-at-age (mm) for chum salmon sampled on the spawning grounds during 1984–85. Sample sizes are given in parentheses. The mean length-at-age for British Columbia chum salmon was derived from Beacham and Murray (1987).

	Male age						Female age					
Population	3		4		5		3		4		5	
Yukon River												
Kluane	509	(19)	516	(59)	556	(4)	490	(25)	501	(87)	526	(2)
Minto	525	(13)	528	(46)	541	(8)	509	(25)	516	(95)	525	(12)
Fishing Branch	477	(5)	524	(64)	548	(5)	487	(10)	504	(74)	519	(19)
Porcupine			541	(41)	546	(4)	462	(1)	514	(16)	531	(5)
Teslin			521	(17)	521	(14)			492	(19)	506	(14)
Koidern			510	(29)	514	(10)			468	(31)	503	(11)
Mean	510	(37)	524	(256)	531	(45)	497	(61)	505	(322)	515	(63)
British Columbia												
Mean	543	(1974)	595	(3186)	621	(344)	532	(1357)	579	(2879)	605	(255)

TABLE 4.—Mean measurements (mm) for six morphometric characters for chum salmon sampled during 1984. Measurements for each individual were standardized to a postorbital-hypural length of 520 mm. Standard deviations are indicated in parentheses. The size (%) of each standardized character relative to body length is indicated for both Yukon and British Columbia chum salmon. Data for 4,862 male and 4,044 female British Columbia chum salmon were standardized to 600 mm postorbital-hypural length and were derived from Beacham and Murray (1987).

	Kluane	Minto	Fishing Branch	% of length Yukon	% of length B.C.
Males					
Head length	79.4 (4.3)	80.7 (3.3)	81.3 (2.9)	15.48	16.02
Caudal peduncle	39.9 (2.8)	41.5 (2.3)	41.2 (2.5)	7.85	8.37
Anal fin base	67.4 (4.4)	70.0 (3.5)	69.3 (4.4)	13.25	13.68
Anal fin height	57.8 (3.9)	59.5 (3.1)	58.7 (4.5)	11.28	11.65
Dorsal fin base	62.9 (5.6)	66.1 (4.0)	63.9 (4.6)	12.34	13.01
Dorsal fin height	88.1 (6.2)	90.2 (5.4)	92.0 (5.6)	17.33	17.64
Sample size	37	32	39		
Females					
Head length	73.5 (4.3)	74.7 (4.0)	76.3 (3.5)	14.38	14.64
Caudal peduncle	37.7 (3.1)	38.9 (3.3)	39.5 (2.2)	7.44	8.06
Anal fin base	67.8 (5.2)	68.0 (4.8)	68.8 (4.8)	13.12	13.79
Anal fin height	56.0 (4.0)	57.6 (4.8)	58.0 (4.5)	11.00	11.65
Dorsal fin base	58.2 (4.1)	58.4 (4.4)	59.1 (4.4)	11.26	11.79
Dorsal fin height	79.8 (6.5)	82.7 (5.3)	84.4 (5.4)	15.83	16.24
Sample size	63	68	61		

British Columbia (Beacham and Murray 1987).

Survival Rates

Embryo survival rates were lowest at a 4°C incubation temperature and highest at 12°C, with significant differences observed among incubation temperatures ($P < 0.05$) (Table 5). Significant differences were also observed in embryo survival rates among families ($P < 0.0$), but not between replicates within families ($P > 0.10$). An interaction between family and incubation temperature occurred ($P < 0.01$), illustrating that trends in embryo survival with respect to incubation temperature were not the same for all families.

Alevin survival rates were uniformly high (Table 5), with no significant difference observed among temperatures, among families, or between replicates within families. The interaction between family and incubation temperature also occurred for alevin survival rates ($P < 0.05$).

TABLE 5.—Survival rates of embryos and alevins for Kluane River chum salmon maintained at constant water temperatures of 4°, 8°, and 12°C. Time of 50% hatching (days) of the alevins and 50% emergence (days) of the fry is also indicated. *N* is number of fertilized eggs (for embryo survival rates) or alevins hatched (for alevin survival rates). Standard deviations of 50% hatching and emergence times are in parentheses.

Temperature (°C)	*N*	Survival rate	Time to 50% hatching or emergence
Embryos			
4.1 (0.28)	2,172	0.767	113.9 (2.3)
8.0 (0.21)	2,387	0.906	65.7 (0.6)
12.0 (0.35)	2,432	0.955	43.7 (0.9)
Alevins			
4.1 (0.29	1,666	0.975	182.2 (1.9)
8.0 (0.20)	2,162	0.998	111.6 (1.2)
12.0 (0.35)	2,323	0.991	79.6 (1.1)

Hatching and Emergence Time

Warmer water temperatures during incubation enhanced the development rate of Kluane River chum salmon (Table 5). Timings of both alevin hatching and fry emergence at a specific incubation temperature were comparable with that of a British Columbia chum salmon population spawning in late December or early January (Beacham and Murray 1986, 1987), nearly three months later than the spawning time of the Kluane River population.

Alevin and Fry Size

Alevin and fry length and weight were influenced by the water temperature during development. The longest and heaviest alevins and fry were observed at 4°C (Table 6). Significant differences in alevin length and weight were observed among incubation temperatures, among families, and between repli-

cates within families (all $P < 0.05$). Significant interactions between temperature and family were also observed for all alevin size characters (all $P < 0.05$), again illustrating that alevin size characters did not respond consistently among families to changes in incubation temperature.

The effect of different incubation temperatures on fry size characters was similar to that for the alevin size characters. Significant differences in fry length, total weight, and tissue weight were observed among temperatures, among families, and between replicates. The amount of yolk remaining at the time of fry emergence was similar at all incubation temperatures ($P > 0.05$) (Table 6). Interactions between family and incubation temperature were present for all fry size characters (all $P < 0.05$).

TABLE 6.—Fork length, total weight, yolk weight, and tissue weight for Kluane River chum salmon alevins and fry maintained at constant 4°, 8°, and 12°C water temperatures. *N* is the number of alevins and fry measured and weighed for all families combined. Standard deviations are in parentheses.

Temperature (°C)	N	Fork length (mm)	Total weight (mg)	Yolk weight (mg)	Tissue weight (mg)
Alevin					
4	150	21.1 (1.4)	222.2 (38.2)	136.9 (19.1)	85.3 (22.4)
8	150	20.8 (0.7)	108.9 (18.9)	106.7 (12.7)	74.2 (8.0)
12	149	20.4 (0.9)	176.6 (20.1)	109.8 (12.9)	66.8 (9.4)
Fry					
4	150	32.3 (1.8)	308.4 (52.9)	30.0 (8.7)	278.4 (51.3)
8	150	31.0 (0.9)	277.5 (27.4)	28.0 (7.2)	249.5 (23.5)
12	150	30.5 (1.1)	277.6 (28.1)	30.7 (6.4)	247.5 (27.2)

Biochemical Genetics

Regional differentiation of allelic frequencies for chum salmon stocks in Alaska and the Yukon Territory was observed. Chum salmon from Alaska generally had a lower frequency of Idh-1^{100} and a higher frequency of Tapep (Lgg)^{75} than those from the Yukon Territory (Table 7). Regional differentiation in allelic frequencies was also observed for the other loci examined. The Delta and Toklat River populations, both tributaries of the Tanana River, had higher frequencies of Idh-3^{100} than all other populations except the Teslin River population. Only one genotypic frequency was not in Hardy-Weinberg equilibrium, that being Pgdh in the Toklat River population. The disequilibrium was due to a heterozygote deficiency.

Variation in allelic frequencies among populations within a region was greater than annual variation in allelic frequencies within a population ($F_{67,48} = 4.00$, $P < 0.01$) (Table 8). Annual stability of allelic frequencies was examined for the loci for which two years of data was available in each population. Of 39 comparisons made, 3 (8%) were significant (Table 8).

Heterozygosity of populations from Alaska was generally higher than that from the Yukon Territory. Mean heterozygosities were 0.156 (SD = 0.009) and 0.138 (SD = 0.019), respectively, for the loci outlined in Table 7. Heterozygosity values are dependent upon the number of polymorphic and monomorphic loci included in the calculations, and thus will vary among studies.

The analysis of genetic distance for all pairwise combinations of the 10 populations sampled ranged from 0.0000 to 0.0072. A dendogram based upon the unweighted pair group mean analysis (UPGMA) illustrated two main clusters of populations (Fig. 2).

FIGURE 2.—Dendogram produced from cluster analysis using Nei's (1978) genetic distance value. Codes are C = Canadian and US = United States.

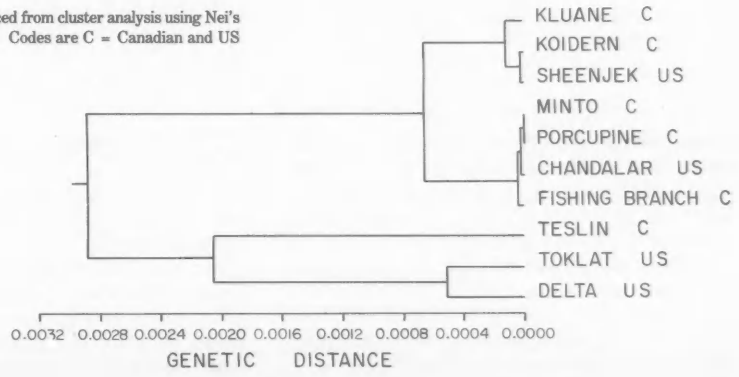

TABLE 7.—Observed allelic frequencies at polymorphic loci for 10 Yukon River drainage and other alleles were assigned numbers

Stock	Year	Idh-1		Idh-3				MdhP	
		N	100	*N*	100	40	85	*N*	100
Kluane	1984	107	1.000	106	0.358	0.585	0.057	107	0.977
	1985	106	1.000	106	0.396	0.552	0.052	106	0.991
	Pooled	213	1.000	212	0.377	0.568	0.054	213	0.984
Minto	1984	130	1.000	130	0.481	0.508	0.012	130	0.904
	1985	114	1.000	114	0.482	0.461	0.057	114	0.899
	Pooled	244	1.000	244	0.482	0.486	0.033	244	0.902
Fishing Branch	1984	126	1.000	126	0.460	0.512	0.028	126	0.944
	1985	99	1.000	98	0.444	0.510	0.046	99	0.914
	Pooled	225	1.000	224	0.453	0.511	0.036	225	0.931
Teslin	1985	90	1.000	90	0.611	0.361	0.028	90	0.889
Koidern	1985	100	1.000	100	0.405	0.570	0.025	100	0.980
Porcupine	1985	81	1.000	81	0.463	0.506	0.031	81	0.938
Toklat	1985	120	0.946	120	0.579	0.350	0.071	120	0.887
	1986	124	0.952	124	0.512	0.399	0.089	124	0.911
	Pooled	244	0.949	244	0.545	0.375	0.080	244	0.900
Delta	1985	146	0.990	145	0.538	0.417	0.045	146	0.877
	1986	147	0.990	146	0.490	0.449	0.062	147	0.884
	Pooled	293	0.990	291	0.514	0.433	0.053	293	0.881
Sheenjek	1985	143	0.993	147	0.398	0.585	0.017	144	0.962
	1986	150	0.987	124	0.415	0.528	0.056	150	0.907
	Pooled	293	0.990	271	0.406	0.559	0.035	294	0.934
Chandalar	1986	147	1.000	143	0.448	0.497	0.056	147	0.939

TABLE 8.—Analysis of heterogeneity of allelic frequencies between countries, among sampled during

Source of variation	Idh-1		Idh-3		MdhP		Mpi	
	df	G	df	G	df	G	df	G
Between countries	1	45.4**	2	12.6**	1	9.6**	1	4.5*
Among populations within countries	8	35.7**	16	77.4**	8	59.2**	8	13.9
Canada	5	0.0	10	34.7**	5	45.2**	5	10.0
United States	3	35.7**	6	42.7**	3	14.0	3	3.9
Between years within populations	6	0.3	12	21.5	6	8.7	6	4.5
Kluane	1	0.0	2	0.6	1	0.6	1	1.3
Minto	1	0.0	2	8.7**	1	0.0	1	0.1
Fishing Branch	1	0.0	2	1.1	1	1.1	1	1.7
Toklat	1	0.0	2	2.3	1	0.5	1	1.2
Delta	1	0.2	2	1.8	1	0.0	1	0.2
Sheenjek	1	0.1	2	7.0	1	6.5**	1	0.0

The Toklat and Delta River populations were distinctive from other populations surveyed. The population from Chandalar River, a tributary of the Porcupine River, was similar to the Porcupine River population (sampled at the Old Crow fishery) and to the Fishing Branch River population, also a tributary of the Porcupine River. The populations from Kluane and Koidern Rivers, tributaries of the White River, were also similar to each other, as well as to the Sheenjek River population in Alaska.

DISCUSSION

Yukon River fall chum salmon undertake the longest freshwater spawning migration of chum salmon in North America and spawn in locations where winter environmental conditions are very severe. They are also relatively abundant, with an average of almost 450,000 chum salmon harvested annually during 1974–83 (Buklis and Barton 1984). Their abundance indicates that they have adapted success-

fall chum salmon populations during 1984–86. The most common allele at a locus was designated 100, according to the mobility relative to that of the 100 allele.

Stock	Year	Mpi		Pgdh		G3pdh-2		Tapep			
		N	100	*N*	100	*N*	100	*N*	100	50	75
Kluane	1984	105	0.910	107	0.991	106	0.887				
	1985	106	0.943	105	0.990	104	0.856	106	0.901	0.099	0.000
	Pooled	211	0.927	212	0.991	210	0.871	106	0.901	0.099	0.000
Minto	1984	130	0.923	130	0.962	130	0.888				
	1985	114	0.934	114	0.956	114	0.842	114	0.842	0.158	0.000
	Pooled	244	0.928	244	0.959	244	0.867	114	0.842	0.158	0.000
Fishing Branch	1984	126	0.893	126	0.960	113	0.854				
	1985	97	0.933	99	0.995	96	0.880	99	0.803	0.197	0.000
	Pooled	223	0.910	225	0.976	209	0.866	99	0.803	0.197	0.000
Teslin	1985	90	0.972	90	0.994	89	0.983	90	0.861	0.139	0.000
Koidern	1985	100	0.945	100	1.000	99	0.879	97	0.845	0.155	0.000
Porcupine	1985	79	0.943	81	0.981	75	0.847	80	0.806	0.194	0.000
Toklat	1985	120	0.917	120	0.971	112	0.848	120	0.808	0.158	0.033
	1986	124	0.883	123	0.976	111	0.833	122	0.852	0.119	0.029
	Pooled	244	0.900	243	0.973	223	0.841	242	0.831	0.138	0.031
Delta	1985	141	0.922	146	0.949	134	0.888	146	0.818	0.147	0.034
	1986	147	0.935	147	0.939	104	0.880	142	0.852	0.106	0.042
	Pooled	288	0.929	293	0.944	238	0.884	288	0.835	0.127	0.038
Sheenjek	1985	150	0.913	144	0.972	129	0.876	150	0.847	0.147	0.007
	1986	150	0.913	148	0.973	120	0.879	149	0.822	0.158	0.020
	Pooled	300	0.913	292	0.973	249	0.878	299	0.834	0.152	0.013
Chandalar	1986	145	0.897	147	0.973	85	0.871	145	0.834	0.148	0.017

populations within countries, and between years within populations for Yukon River fall chum salmon 1984–86. $P < 0.01$; $P < 0.05$.

Source of variation	Pgdh		G3pdh-2		Tapep		Total		Standardized F-statistic
	df	G	df	G	df	G	df	G	
Between countries	1	7.9*	1	0.7	2	48.3**	9	129.0**	14.33
Among populations within countries	8	32.0**	8	34.6**	11	20.6*	67	273.4**	4.08
Canada	5	22.6*	5	30.3*	5	10.3	40	153.1**	3.83
United States	3	9.4	3	4.3	6	10.3	27	120.3**	4.46
Between years within populations	6	5.1	6	3.0	6	5.8	48	48.9	1.02
Kluane	1	0.2	1	0.6					
Minto	1	0.0	1	1.9					
Fishing Branch	1	4.8**	1	0.4					
Toklat	1	0.0	1	0.1	2	1.7			
Delta	1	0.1	1	0.0	2	1.8			
Sheenjek	1	0.0	1	0.0	2	2.3			

fully to a long distance freshwater migration and extreme winter conditions.

Several biological characters differ between chum salmon in the Yukon River and in British Columbia. For Yukon River fall chum salmon, approximately equal numbers of salmon mature, on average, at three and five years of age, although there is annual variation (Buklis and Barton 1984). In the Amur River, fall chum salmon mainly mature at four and five years of age (Smirnov 1975). Similar results were recorded in our study. Yukon River chum salmon matured at older ages and at smaller mean lengths-at-age than did chum salmon in British Columbia. A general trend of younger ages at maturity and increased mean lengths-at-age in southern as compared with northern chum salmon populations has been reported by Salo (in press). This trend may be a result of the earlier timing of fry emergence and later timing of adult spawning of more southern populations, allowing more time for

ocean growth, particularly in the year of maturity.

Body shape of Yukon River and British Columbia chum salmon was different, with Yukon River chum salmon having a shorter head, thinner caudal peduncle, and smaller fins than British Columbia chum salmon. This more fusiform body shape is presumably an adaptation to the long migration in fresh water, as selection should result in a body shape that would minimize energy consumption during migration. Morphological differentiation with respect to distance of upstream migration has been reported to occur in other *Oncorhynchus* species (Eniutina 1954; Taylor and McPhail 1985), as well as with respect to river size (Hjort and Schreck 1982; Beacham and Murray 1987).

The mean fecundity of 2,325 eggs per female for Yukon River fall chum salmon reported in our study is similar to other results. Elson (1975) reported mean fecundities of 2,360 eggs and 2,513 eggs per female for Porcupine River chum salmon sampled in 1971 and 1973, respectively. Raymond (1981) reported mean fecundities of Tanana River chum salmon of 2,355 eggs in 1977 and 2,762 eggs in 1978. Fecundities of Yukon River fall chum salmon are less than those reported for many chum salmon stocks in British Columbia (Beacham 1982), and also less than fall chum salmon in the Amur River (3,200 to 4,300 eggs) (Smirnov 1975). Mean egg size of Yukon River fall chum salmon is also less than that of Amur River chum salmon (180 to 300 mg, 6.7 to 9.0 mm diameter) (Smirnov 1975).

The different fecundities and ages at maturity of Yukon River and British Columbia chum salmon present an interesting contrast in life history characters. Yukon River fall chum salmon mature at an average age of 0.28 years older than British Columbia salmon, which means that they incur an additional 5% mortality if the instantaneous mortality rate during the last year of life for chum salmon is 0.013 per month (Ricker 1976). The lower fecundity and older age at maturity of Yukon River salmon indicate that they are not as productive as chum salmon in British Columbia or that mean survival rates of the two groups are not equivalent. Egg-to-fry survival rates for Yukon River chum salmon have been reported as a mean of about 2.5% (Buklis and Barton 1984), whereas those for British Columbia chum salmon average about 10% (Bakkala 1970; Beacham and Starr 1982). If Yukon River chum salmon are as productive as those in British Columbia, then ocean survival rates of Yukon River chum salmon must be higher than those of British Columbia chum salmon.

When incubated under the same water temperatures, Yukon River chum salmon alevins hatch and the fry emerge sooner than most chum salmon populations in British Columbia (Beacham and Murray 1987). The faster development rates presumably occur as a response to lower water temperatures during the winter in the Yukon River tributaries than in rivers in British Columbia. Yukon River chum salmon alevins and fry are shorter and lighter than those from British Columbia (Beacham and Murray 1987), presumably reflective of smaller initial egg size of Yukon River chum salmon. At incubation temperatures of 4°, 8°, and 12°C, maximum alevin and fry size for Yukon River chum salmon was observed at 4°C, but for British Columbia stocks, maximum alevin and fry size was generally observed at 8°C. These results suggest that Yukon River chum salmon are better adapted for development under low water temperatures than are British Columbia chum salmon.

Yukon River chum salmon are generally distinctive in electrophoretic characteristics from chum salmon in Cook Inlet in Alaska (Okazaki 1981) and British Columbia (Okazaki 1981; Beacham et al. 1985, 1987). For example, the allelic frequency of Idh-3^{25} is 0.28 in Queen Charlotte Islands populations and 0.17 in populations in northern British Columbia (Beacham et al. 1987), but this allele was not detected in our study of Yukon River chum salmon. Heterozygosity of Yukon River chum salmon was lower than that observed for British Columbia salmon (the same loci were included in the analysis) (Beacham et al. 1987). Kijima and Fujio (1984) reported that average heterozygosity is related to effective population size in Japanese chum salmon populations, with more abundant populations having increased genetic variance. Abundance of the Yukon River populations examined in our study is unknown, but the catch data suggest that the individual Yukon River populations may not be as abundant as major chum salmon populations in British Columbia.

Allelic frequencies for most salmon populations are reported to show little annual variation (Grant et al. 1980; Utter et al. 1980; Beacham et al. 1985, 1987), allowing for pooling of samples from a particular population over several years. It should thus not be necessary to conduct annual sampling in order to characterize the populations contributing to fisheries. Stock identification based on stable traits, such as allelic frequencies, reduces annual sampling costs for the baseline stocks. This differs from scale analysis, in which variation in the char-

acters used for stock identification makes annual sampling of the baseline stocks necessary (e.g., Wilcock and McBride 1983; Wilcock 1984), and restricts the incorporation of results into management decisions during the fishing season.

ACKNOWLEDGMENTS

The extensive field sampling necessary for this program was accomplished with the help of many individuals, including Art Demsky, Peter Etherton, Robbin Hunka, Tom Hurds, and especially Wally Barner. Special thanks are due to Bill Arvey, Larry Buklis, and other members of the Alaska Department of Fish and Game for sampling of Alaskan populations. Age determination of chum salmon from scales was conducted by Yvonne Yole. Maintenance and supervision of the incubation laboratory was provided by Wally Barner, Bill Andrews, and Bruce Patten. July Dawes, Brenda Hoitsma, and Tracey Briggs weighed and measured the chum salmon eggs, alevins, and fry examined in this study. The electrophoretic analysis was conducted by Helix Biotech Ltd. of Richmond, B.C., under contract to the Department of Fisheries and Oceans.

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FOOD HABITS AND DAILY RATION OF GREENLAND HALIBUT, *REINHARDTIUS HIPPOGLOSSOIDES*, IN THE EASTERN BERING SEA

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ABSTRACT

This study shows that diet of Greenland halibut varies mainly by depth and size, and that size of prey fish increases as the Greenland halibut increases in size. A total of 1,333 Greenland halibut (or turbot), *Reinhardtius hippoglossoides*, stomachs were collected in the eastern Bering Sea from May 1983 to November 1985 and analyzed. Stomach content data were divided into four groups based on sample location (depth). Using length of the sample animals within each depth group, data were further divided into five size groups. Walleye pollock, *Theragra chalcogramma*, was the most important prey (58% by weight of the total stomach content). Squids (mainly *Berryteuthis* sp.) were the second most (20% by weight) important food of Greenland halibut. Zoarcids and some deep-water fishes (e.g., bathylagids, myctophids, macrourids) were also important food for Greenland halibut 30–69 cm long. Euphausiids were only important as food (64% by weight) of the fish <20 cm collected in the continental shelf <200 m deep. Fishes ≥70 cm fed almost exclusively on fish in all depth areas.

Variation in mean stomach content weight throughout the day was used to determine the diel feeding pattern; from this it appears that Greenland halibut is a continuous feeder. Daily rations (% of body weight per day) of Greenland halibut were calculated using an exponential gastric evacuation rate model. Fish ≥70 cm had a higher daily ration value (1.17% of body weight per day) than did those of the two smaller size groups (0.66 and 0.64% of body weight per day for 30–49 and 50–69 cm size groups, respectively).

Greenland halibut (or turbot), *Reinhardtius hippoglossoides*, is an amphiboreal fish, occurring in both the North Atlantic and the North Pacific, but not in the intervening Arctic Ocean (Hubbs and Wilimovsky 1964). Within this range, the species has been most extensively studied in the Atlantic Ocean. In the Pacific Ocean, Greenland halibut has been found from Baja California (Schmidt 1934), Oregon (Niska and Magill 1967), and Vancouver B.C. (Westrheim and Pletcher 1966), through the Bering and Okhotsk Seas (Shmidt 1950), to Honshu Island, Japan (Hart 1973), but the center of abundance is in the eastern Bering Sea area.

Data of the resource assessment surveys (from 1979 to 1985) in the eastern Bering Sea performed by the Northwest and Alaska Fisheries Center (NWAFC), National Marine Fisheries Service (NMFS), show that Greenland halibut ranked between 5th and 12th place in terms of relative abundance (kg/ha) among the groundfish species; however, it is the most abundant species in continental slope areas (Bakkala 1986[2]).

These assessments suggest that Greenland halibut is a key member of the eastern Bering Sea ecosystem. The importance of this species in predator-prey relationships of this ecosystem is poorly understood since little is known about its food habits and food consumption rate. Food habits of Greenland halibut in the North Atlantic have been studied by Bowering and Lilly (1985) and Haug and Gulliksen (1982). In the eastern Bering Sea, Mikawa (1963), Mito (1974), Smith et al. (1978), and Livingston et al. (1986) reported stomach contents analysis of the Greenland halibut, but the sample sizes in these studies were small and the analyses were limited. The objective of this study is to provide a description of the food habits of Greenland halibut in the eastern Bering Sea, including diel, spatial, and seasonal variations in stomach contents; influence of predator size; and daily ration.

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[2]Bakkala, R. G. 1986. Greenland turbot—biological report. Unpubl. manuscr., 21 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

Manuscript accepted June 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

METHODS AND MATERIALS

Sample Collection and Stomach Content Analysis

Stomachs from 1,333 Greenland halibut were collected from May 1983 to November 1985 in the eastern Bering Sea area (Fig. 1) from NMFS research vessels and foreign commercial fishing vessels (through the U.S. Foreign Fisheries Observer Program). A bottom trawl was the only sampling gear used, and trawl samples were taken throughout the day and night. Due to the low abundance of Greenland halibut in the shelf area (<200 m), stomachs were taken from virtually all Greenland halibut encountered in trawl catches. Random size-stratified samples were obtained from the catches in the slope area. Captured fish were checked in the field for signs of regurgitation and were discarded when there was evidence of food items in the mouth or gill plates or of flaccid stomachs. Stomachs from the sampled fish were excised and put into cloth bags with a specimen label containing fork length, sex, and station information, and were preserved in 4% formaldehyde solution. Individual fish weights were not recorded at sea, but were estimated by using the weight-length equation,

$$W(g) = 0.0060717 \times L(\text{cm})^{3.08864}, \quad (1)$$

estimated from the Greenland halibut data base of the Resource Assessment and Conservation Engineering (RACE[3]) Division of the NWAFC.

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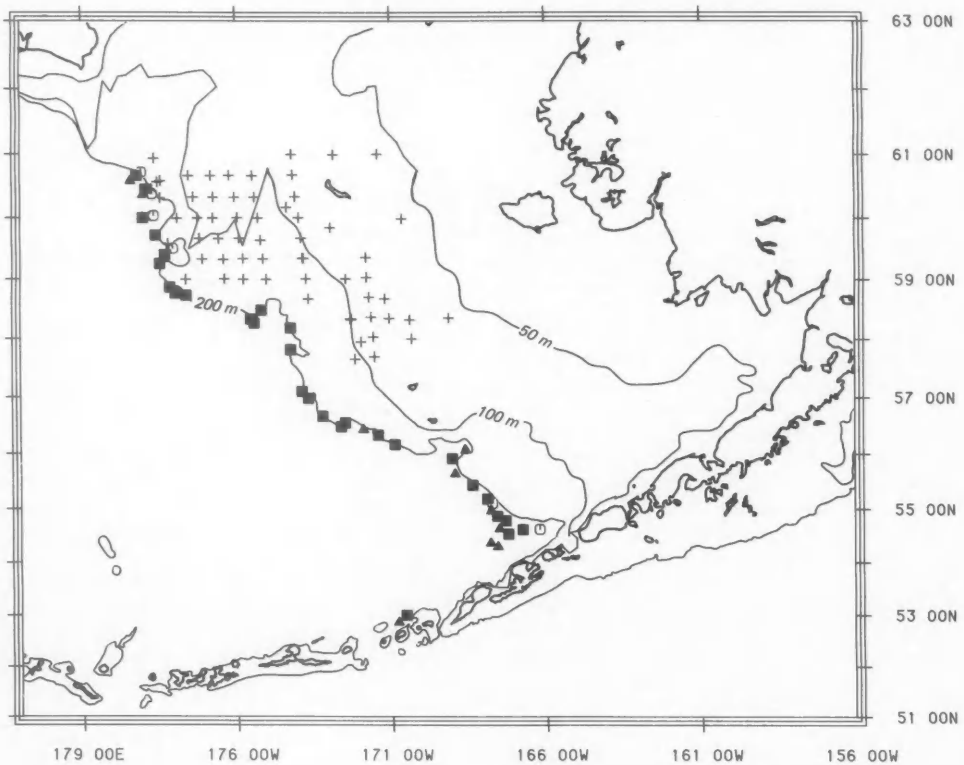

FIGURE 1.—Sampling locations for Greenland halibut in the eastern Bering Sea by four different depth strata, <200 m (+), 200–399 m (O), 400–599 m (■), and ≥600 m (▲).

Stomachs were analyzed individually in the laboratory. Prey items were identified to the lowest possible taxonomic level and counted. Wet weights of the prey items were recorded to the nearest milligram after blotting with paper towels. The fork lengths of prey fish were also measured.

Diet Description

Since the depth distribution of Greenland halibut in this study was broad (from 62 m to 891 m), stomach content data were first subjectively divided by 100 m depth groups. For each 100 m depth class, percent frequency of occurrence (%FO) of prey items, percentage of total stomach content weight (%W) by prey type, and the percentage of total prey number (%N) by prey type were calculated by using ECO/INDEX, a computer program for calculating feeding ecology indices (Vodopovich and Hoover 1981). Based on similarities of major prey items (using percent by weight), stomach content data were combined into four depth groups for analysis: Depth 1 (<200 m), Depth 2 (200–399 m), Depth 3 (400–599 m), and Depth 4 (≥600 m).

Within each of the four depth groups, data were subjectively divided by fish length into 10 cm size groups. By comparing percent by weight of the major prey categories (e.g., gadids, squids) for each size group, the fish within each of the four depth groups were finally lumped into five size groups: <20 cm, 20–29 cm, 30–49 cm, 50–69 cm, and ≥70 cm. Seasonal breakdowns of stomach contents by depth and predator size group could not be performed due to insufficient sample sizes.

Diel Feeding Pattern

Because of the small sample size of fish <30 cm long, only data from three size groups (30–49 cm, 50–69 cm, ≥70 cm) were used for diel feeding analysis. For each size group, the stomach content weights as percent of body weight were calculated for each 3-h period of the 24-h day. Any possible seasonal variations of the diel feeding pattern could not be analyzed because of insufficient seasonal samples.

Daily Ration

In this study, daily ration was calculated using Elliott and Persson's (1978) model. The basic assumption of this model are that the rate of gastric evacuation (R) is exponential and temperature dependent. If stomach samples are taken at fixed intervals of t hours, the mean stomach content weight as a percentage of fish weight (S_i) in each interval (i) is calculated for a total of m intervals over the 24-h period. According to Elliott and Persson (1978), the daily ration ($D.R.$) in terms of percentage of body weight is therefore given by

$$D.R. = \frac{Rt}{1 - \exp(-Rt)} \sum_{i=1}^{m} S_i \,(1 - \exp(-Rt))$$

$$= 24\,\bar{S}R \qquad (2)$$

where $\bar{S} = \sum S_i/m$. Elliott (1972) found the general relationship between R and temperature (T) was exponential:

$$R = ae^{bT}. \qquad (3)$$

Based on data presented in the literature for the normal temperature range of both freshwater and marine fishes, Durbin et al. (1983) concluded that the slope (b) is fairly constant for different prey types and fish species (mean = 0.115), while the intercept (a) changes with prey type and can be estimated from gastric evacuation rate experiments. Since there were no gastric evacuation rate data available for Greenland halibut, results of gastric evacuation experiments on walleye pollock, *Theragra chalcogramma*, feeding on juvenile pollock and squid were used (Dwyer et al. 1987). Although walleye pollock is taxonomically very different from Greenland halibut, these two species have some prey in common. In addition, both species are active, off-bottom feeders which could be expected to be more similar in terms of metabolic rates than benthic feeding, small mouth flounders whose food intake has been studied more extensively. The intercept "a" in Equation (2) was 0.0143 for juvenile walleye pollock and 0.0079 for squid. For this study, the intercept for walleye pollock prey was used to calculate daily ration when fish was the main prey (>70% of diet by weight), and the intercept for squid was used when squid was the main prey. If the diet was split evenly between fish and squid prey, daily ration was calculated using both intercept values to obtain a likely range of daily ration values.

Average bottom temperatures for the eastern Bering Sea for this study were estimated from oceanographic data on the Bering Sea (Ingraham

1983[4]). Because of the small differences in temperatures between different seasons (e.g., 2.90°C, 2.47°C, and 2.93°C were the average temperatures for spring, summer, and autumn at locations where fish 30–49 cm were collected), and the lack of samples for fish <30 cm, daily rations were calculated for three size groups (30–49 cm, 50–69 cm, and ≥70 cm) with all seasons combined. Temperatures used for each of the three size-groups were calculated by matching the haul locations of each size group in our study with the long-term monthly mean bottom temperature at those positions and calculating the average bottom temperature.

RESULTS

General Description of Diet

Stomachs from 1,333 Greenland halibut were analyzed; of these, 610 stomachs (46%) were empty. The size of the Greenland halibut ranged from 9 to 99 cm (fork length) with a mean of 56 cm. The sampling depth ranged from 62 to 891 m with most of the samples (55%) collected from the area 400–599 m deep.

Prey consumed included gastropods, cephalopods, crustaceans, ophiuroids, and fish (Table 1). Twelve families of fish and at least 14 different fish species were represented in the stomach contents. Fish dominated the contents in terms of frequency of occurrence, number, and weight; walleye pollock was the most important fish species consumed with respect to all three measures of prey importance. Three genera of squid were consumed (mainly *Berryteuthis* sp.) and were the second most important prey. The importance of the various prey species or groups (e.g., gadids, squids) changes with bottom depth and Greenland halibut size. Those changes will be discussed in the following sections.

Spatial and Size Differences

Depth 1 (<200 m)

Gadids constituted more than 87% by weight of the stomach contents of all but the smallest (<20 cm) size group (Fig. 2A). Euphausiids comprised 64% by weight (54% by number) of the diet of Greenland halibut <20 cm long. In size group 20–29 cm, the percentage by number of euphausiids was still high (52%), but the percentage by weight decreased dramatically to only 2%. Gadids were the dominant prey for size groups larger than 30 cm in Depth 1 in terms of percent of frequency of occurrence, percent of total stomach contents weight, and the percent of prey number. Cephalopods, clupeids, osmerids, stichaeids, myctophids, and macrourids were not important food items at this depth.

Depth 2 (200–399 m)

No Greenland halibut smaller than 30 cm were collected at this depth range. Cephalopods, in terms of the three diet measures shown in Figure 2B, were the dominant food items found in the size groups 30–49 cm and 50–69 cm. On the other hand, gadids were the dominant prey in size group ≥70 cm (Fig. 2B). When all sizes were combined, the cephalopods were more important than gadids (Fig. 2B, lower right); however, when the size groups were separated (Fig. 2B), the different contribution of gadids and cephalopods to different size groups is very clear (cephalopods are most important for fish <70 cm and gadids are important for fish ≥70 cm). Miscellaneous prey fishes found in the entire Depth 2 group included zoarcids, bathylagids, myctophids, and pleuronectids.

Depth 3 (400–599 m)

No stomachs of Greenland halibut smaller than 30 cm were collected in this depth range (Fig. 2C). For Greenland halibut 30–49 cm long, zoarcids (38.6%) were the most important prey item in terms of percentage by weight of the stomach contents, followed by cephalopods (30.7%) and gadids (17%). In terms of percent of prey number, cephalopods comprised 39% of the total prey in this size group, followed by gadids (22%), bathylagids (17.3%), and zoarcids (8.7%). For the size group 50–69 cm, cephalopods, gadids, and zoarcids comprised 61, 21, and 12% by weight of the stomach contents, respectively. Cephalopods also comprised the highest percentage (35%) by the number in this size group. Gadids were the dominant prey of large Greenland halibut (≥70 cm). They comprised 87% by weight, 69% by number, and 82% by frequency of occurrence of the stomach contents of this size group (Fig. 2C). Other prey fishes found in the Depth 3 group included stichaeids, myctophids, cottids, macrourids, cyclopterids, and pleuronectids. For the Depth 3 group (Fig. 2C, lower right), gadids were the domi-

[4]Ingraham, W. J. 1983. Temperature anomalies in the eastern Bering Sea 1953–82. NWAFC Processed Rep. 83-21, 348 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

TABLE 1.—Prey items found in the stomachs of Greenland halibut collected in the eastern Bering Sea during summer 1983 through fall 1985. %FO = percent frequency of occurrence, %*N* = percent by number, %W = percent by weight, t = <0.01% W.

Prey item	%FO	%*N*	%W
Gastropoda			
Buccinum sp.	0.4	0.34	0.14
Cephalopoda	31.9	22.67	20.28
Teuthoidea	30.8	21.98	19.65
Gonatidae	10.5	8.16	11.64
Gonatopsis sp.	1.9	1.20	2.97
Gonatus sp.	0.7	0.60	0.13
Gonatus magister	0.1	0.26	0.09
Berryteuthis sp.	6.4	4.81	6.69
Berryteuthis magister	0.3	0.26	1.03
Unidentified Gonatidae	1.4	1.03	0.73
Unidentified Teuthoidea	20.5	13.82	8.01
Octopoda	0.1	0.09	0.51
Unidentified Cephalopoda	1.0	0.60	0.12
Crustacea	7.8	12.39	0.41
Mysidacea	2.2	1.64	0.01
Gnathopausia gigas	0.7	0.52	t
Holmesiella anomala	1.0	0.77	t
Pseudomma truncatum	0.1	0.09	t
Unidentified Mysidacea	0.4	0.26	t
Cumacea	0.1	0.17	t
Amphipoda	1.2	1.54	t
Gammaridea	1.0	0.77	t
Hyperiidea			
Parathemisto libellula	0.3	0.77	t
Euphausiacea	1.8	4.90	t
Thysanoessa inermis	1.2	3.78	t
Unidentified Euphausiacea	0.6	1.12	t
Decapoda			
Caridea	2.4	3.79	0.15
Pasiphaeidae			
Pasiphaea pacifica	0.1	0.09	t
Hippolytidae	0.4	2.58	0.06
Eualus sp.	0.3	2.06	0.04
Eualus biunguis	0.3	0.52	0.02
Panadalidae	1.2	0.78	0.08
Pandalus sp.	0.8	0.52	0.04
Pandalopsis dispar	0.3	0.17	0.03
Unidentified Pandalidae	0.1	0.09	0.01
Crangonidae			
Crangon communis	0.3	0.17	0.01
Unidentified Caridea	0.3	0.17	t
Reptantia	0.4	0.27	0.25
Anomura			
Paralithodes sp.	0.1	0.09	0.14
Brachyura	0.3	0.18	0.11
Chionoecetes sp.	0.1	0.09	0.08
Chionoecetes opilio	0.1	0.09	0.03
Unidentified Crustacea	0.1	0.09	t
Ophiuroidea	1.1	1.81	t
Ophiurida	1.0	1.72	t
Unidentified Ophiuroidea	0.1	0.09	t
Larvacea Copelata	0.4	0.69	t
Teleostei	71.7	61.36	77.93
Clupeidae			
Clupea pallasii	0.3	0.17	0.74
Osmeridae	0.1	0.09	t
Bathylagidae	7.6	8.24	0.63
Leuroglossus stilbius	0.4	0.43	0.04
Unidentified Bathylagidae	7.2	7.81	0.59
Myctophidae	5.0	6.87	0.71
Stenobrachius leucopsarus	0.1	0.09	t
Unidentified Myctophidae	4.8	6.78	0.71
Gadidae	32.7	26.35	61.08
Theragra chalcogramma	28.2	23.35	58.39
Unidentified Gadidae	4.4	3.00	2.69
Zoarcidae	5.0	4.13	3.51
Lycodes sp.	4.1	3.52	2.95
Lycodes diapterus	0.1	0.09	0.05
Lycodes palearis	0.1	0.09	0.11
Unidentified Zoarcidae	0.6	0.43	0.40
Macrouridae	1.0	1.12	2.00
Coryphaenoides sp.	0.7	0.43	0.39
Coryphaenoides filifer	0.1	0.09	0.04
Unidentified Macrouridae	0.8	0.60	1.57
Icelidae			
Icelus spiniger	0.1	0.09	0.03
Cottidae	0.2	0.18	0.21
Dasycottus setiger	0.1	0.09	0.20
Hemitripterus boline	0.1	0.09	0.01
Cyclopteridae	0.6	0.35	1.73
Aptocyclus ventricosus	0.1	0.09	0.55
Careproctus cypselurus	0.1	0.09	0.82
Unidentified Cyclopteridae	0.3	0.17	0.36
Stichaeidae	0.7	0.43	0.09
Lumpenus maculatus	0.3	0.17	0.04
Unidentified Stichaeidae	0.4	0.26	0.05
Pleuronectidae			
Reinhardtius hippoglossoides	0.6	0.34	1.60
Unidentified Teleostei	20.6	12.88	5.02
Unidentified organic material	0.3	0.17	t
Total number of stomachs	1,333		
Total stomachs with food	723		
Total prey weight (g)	47,713.52		
Total prey number	1,165		

nant prey in the diet due to the consumption of walleye pollock by Greenland halibut ≥70 cm; however, cephalopods and other fishes were more important than gadids for the two smaller size groups.

Depth 4 (≥600 m)

No stomachs were collected for fish smaller than 30 cm in this depth group (Fig. 2D). For size groups 30–49 cm, cephalopods were the dominant prey (56%) of Greenland halibut in terms of percent by weight, followed by bathylagids at 29%. However, the percent of number and the percent of frequency of occurrence of bathylagids (FOG in Figure 2D, upper left) were higher than those of the cephalopods. The stomach contents (by weight) of Greenland halibut 50–69 cm long was composed of 57% cephalopods, 22% macrourids, 12% bathylagids, 4%

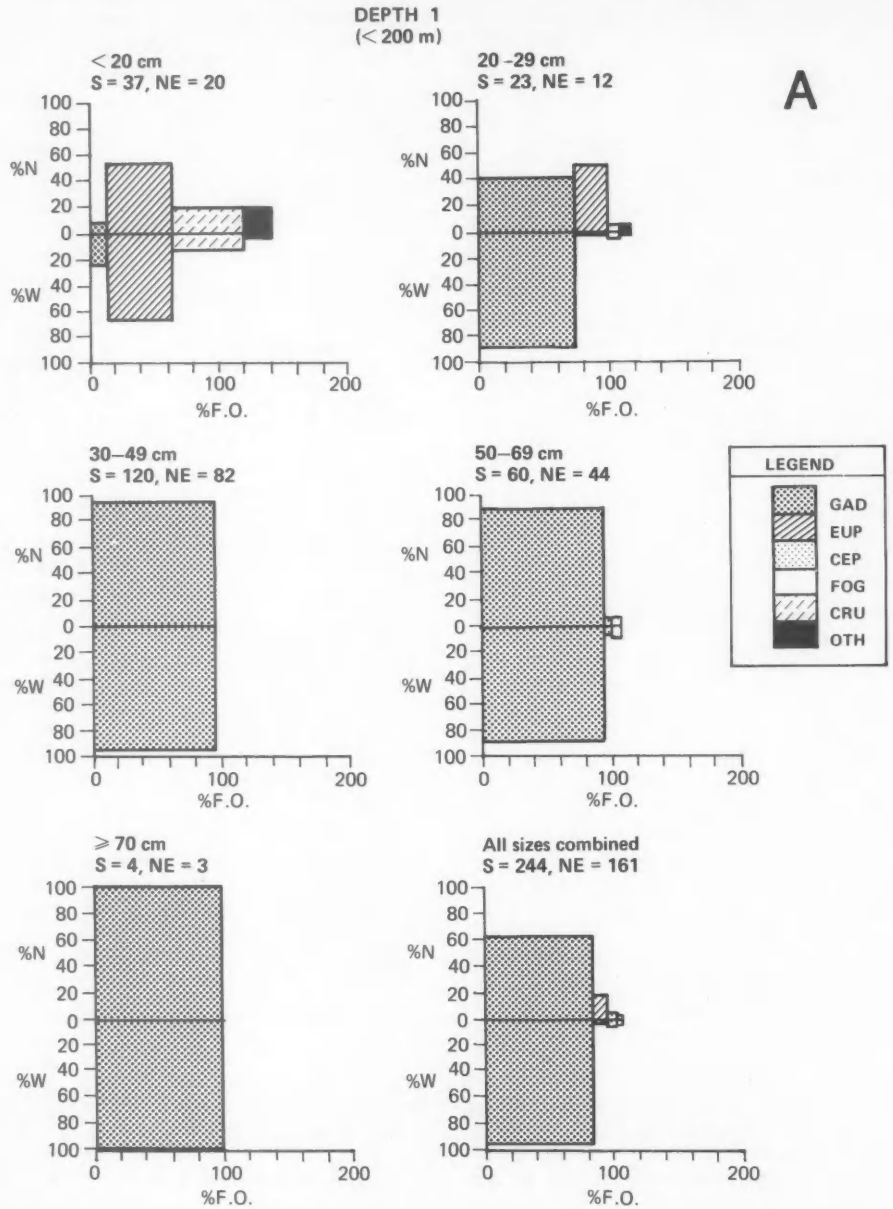

FIGURE 2.—Percent of frequency of occurrence (%FO), percent of prey number (%*N*), and percent of stomach content weight (%W) of major prey items in the stomach contents of Greenland halibut (by depth and by size). S, total number of stomachs; NE, nonempties; %FO, GAD, Gadids; EUP, Euphausiids; CEP, Cephalopod; FOG, Fish other than gadids; CRU, Crustacean; OTH, Others. A) Depth 1.

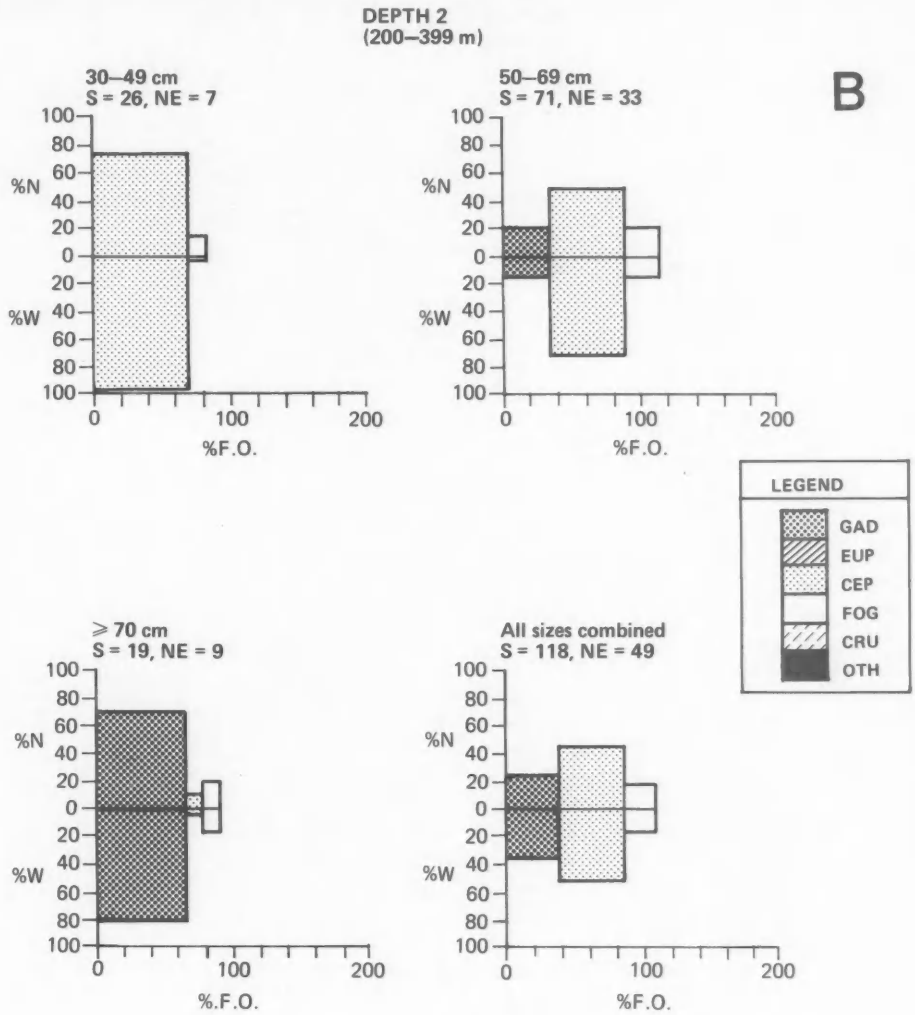

FIGURE 2.—*Continued.*—B) Depth 2.

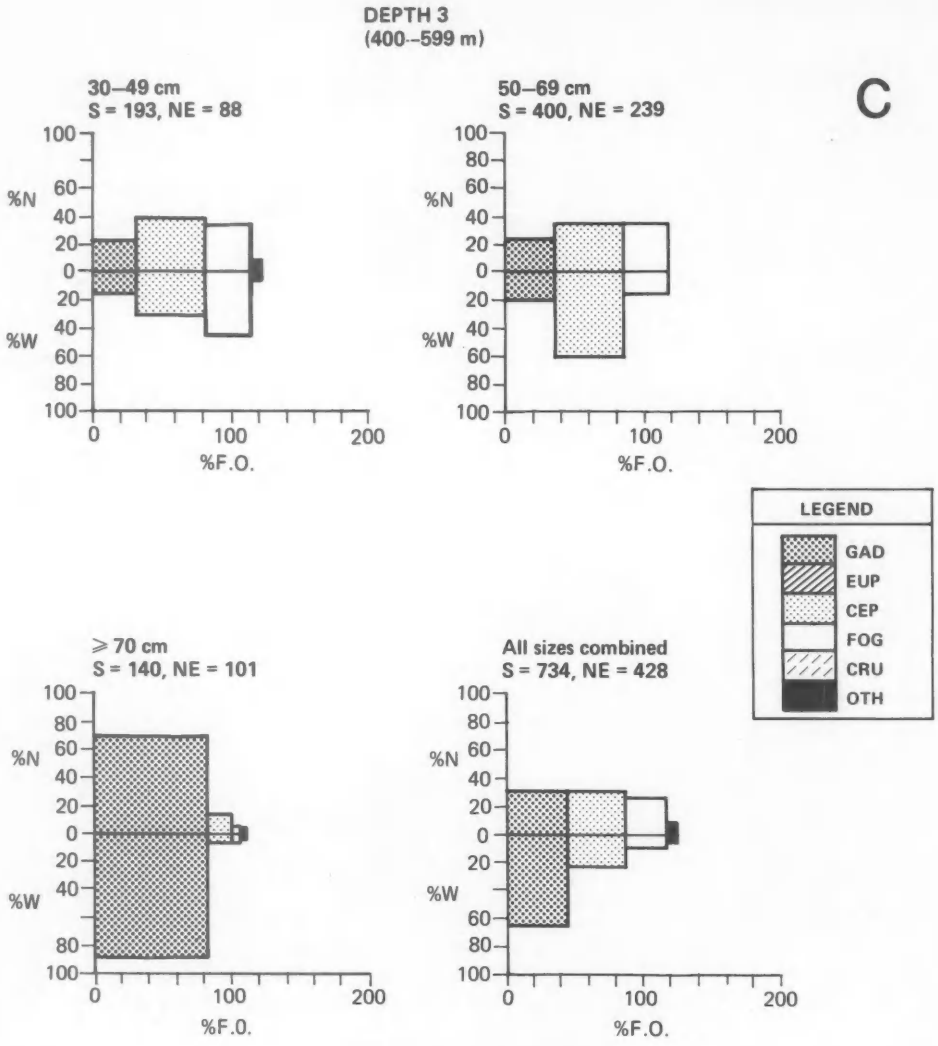

FIGURE 2.—*Continued.*—C) Depth 3.

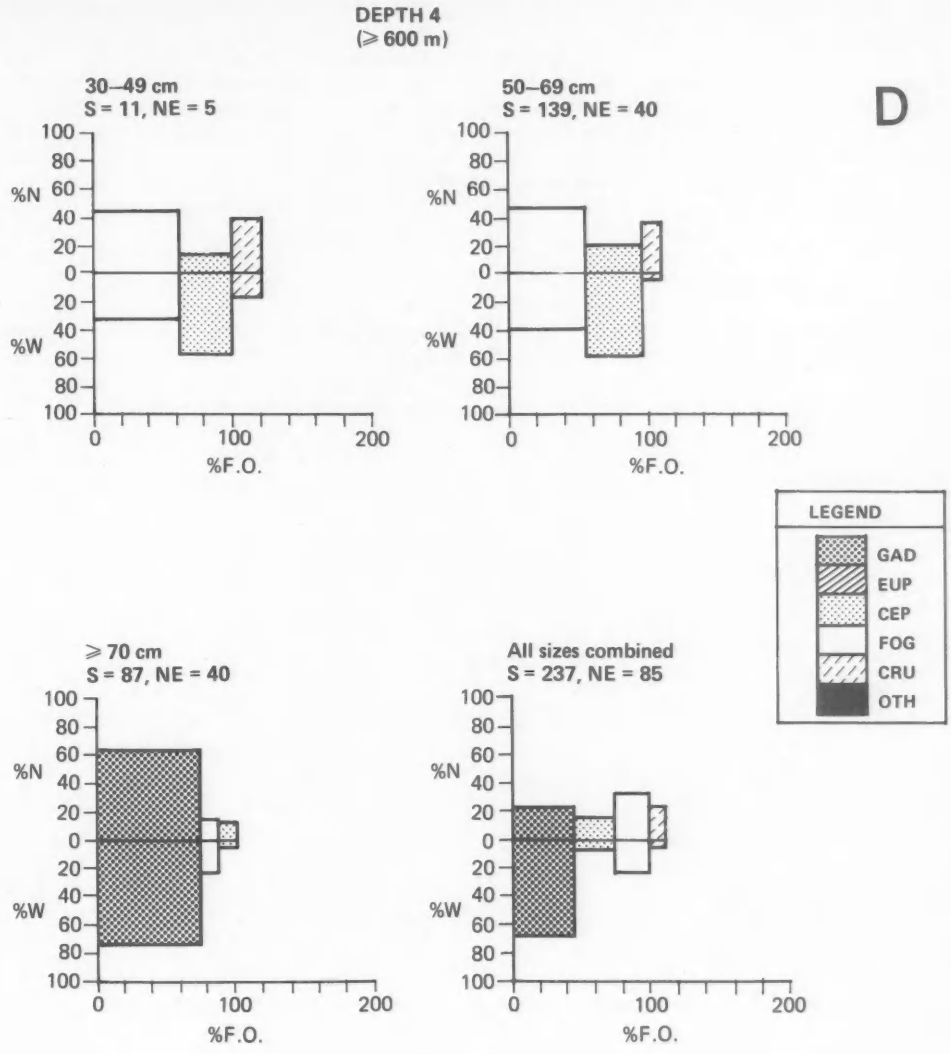

FIGURE 2.—*Continued.*—D) Depth 4.

myctophids, and 0.6% stichaeids. In terms of percent by number and the percent of frequency of occurrence, the fishes other than gadids (FOG in Figure 2D) were more important than the cephalopods. No gadids were found in either the 30–49 cm group or the 50–69 cm group of fishes; however, they were the dominant prey (75% by weight, 64% by number, and 73% by frequency of occurrence) of Greenland halibut ≥70 cm (Fig. 2D, lower left) as in the other three depth groups (Fig. 2A,B,C, lower left). Other food in this size group included macrourids, cyclopterids, and pleuronectids. Even though gadids did not occur in the two smaller size groups, they were important in the Depth 4 group as a whole (Fig. 2D, lower right).

Trends in Fish Consumption

The size of the walleye pollock consumed by Greenland halibut increased dramatically with predator size (Fig. 3). The relationship appears linear with $r^2 = 0.835$. Based on the age-length key for walleye pollock (Halliday and Umeda 1986), the walleye pollock eaten by Greenland halibut were approximately age 0 and age 1 for smaller size fish (<50 cm), age 1 and age 2 for medium size fish (50–69 cm), and age 3 and age 4 for the fish ≥70 cm (Fig. 4).

The importance of prey fishes in the diet of Greenland halibut appears to be depth related (Table 2). Clupeids disappear from the diet in waters ≥200 m deep, while gadids are important in all depths but occur most frquently (85%FO), and comprise most of the diet both in number and weight (65% and 93%, respectively), in the area <200 m deep. Zoarcids appear in stomachs only in the area 200–600 m deep, and bathylagids start appearing at 200–399 m and increase in importance as the water depth increases. Myctophids seem to be more important in the area 400–599 m than in the other depths,

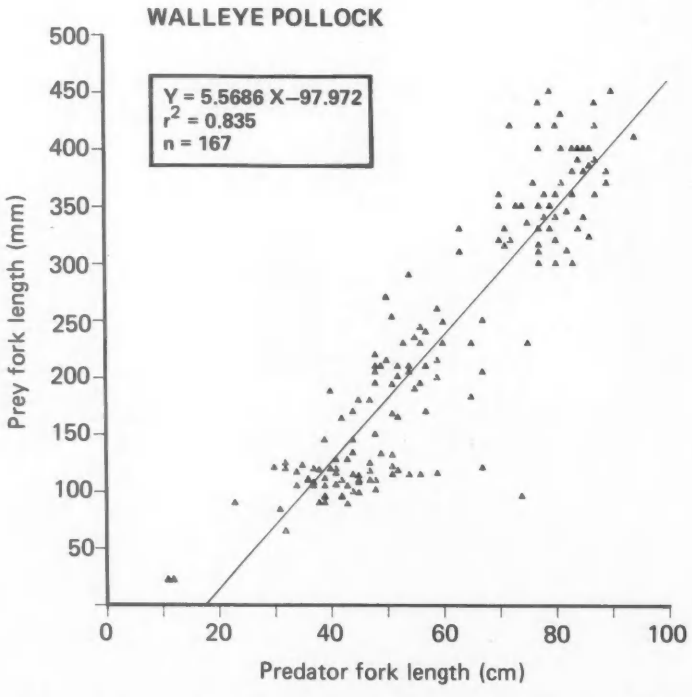

FIGURE 3.—Scatter plot of the fork length of walleye pollock that were consumed by Greenland halibut of different sizes in the eastern Bering Sea.

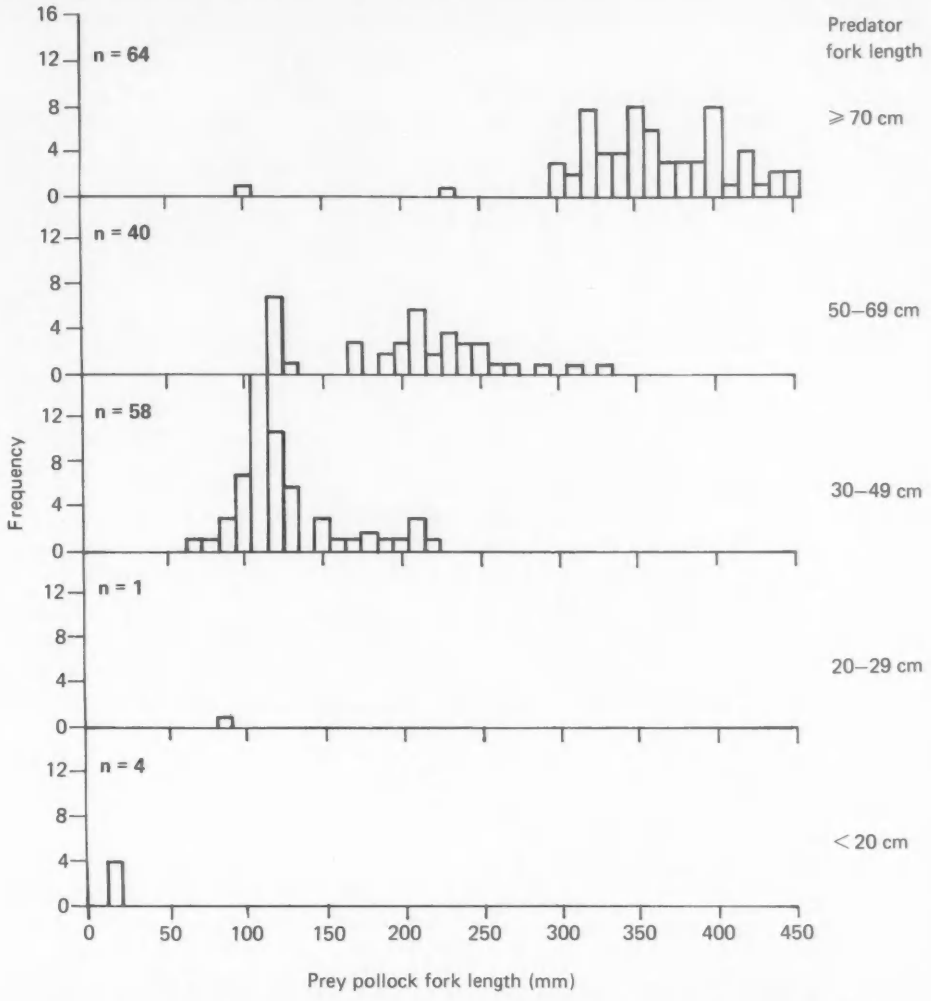

FIGURE 4.—Length-frequency distributions of walleye pollock consumed by Greenland halibut in the eastern Bering Sea.

while macrourids are important prey in even deeper waters (⩾600 m).

Trends in Stomach Fullness

Fewer empty stomachs were found in summer than in spring and autumn except in the ⩾70 cm size group (Fig. 5). The occurrence of empty stomachs for all size groups was about 35% in summer and 50% in autumn. In spring, samples from the 30–49 cm size group had the greatest percentage of empty stomachs (about 70%), followed by size groups 50–69 cm (about 58%) and ⩾70 cm (about 12%).

There were no apparent diel trends in stomach content weight in this study (Fig. 6). The stomach content weight (expressed as percentage of body weight) for large fish (⩾70 cm) was fairly constant except for the 0900–1200 h time period. The

TABLE 2.—Importance of the prey fish by depth found in the stomachs of Greenland halibut collected from the eastern Bering Sea. %FO = percent frequency of occurrence, %*N* = percent by number, %W = percent by weight.

	Depth 1 (<200 m)			Depth 2 (200–399 m)			Depth 3 (400–599 m)			Depth 4 (≥600 m)		
Prey fish	%FO	%*N*	%W	%FO	%*N*	%W	%FO	%*N*	%W	%FO	%*N*	%W
Clupeidae	0.6	0.3	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Osmeridae	0.6	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stichaeidae	1.2	0.7	0.4	0.0	0.0	0.0	0.5	0.3	0.1	1.2	0.7	0.1
Gadidae	85.1	64.9	92.7	36.7	26.5	36.2	45.3	31.4	64.4	42.4	25.2	67.9
Zoarcidae	0.0	0.0	0.0	8.2	8.8	7.0	7.4	6.5	4.8	0.0	0.0	0.0
Bathylagidae	0.0	0.0	0.0	6.1	5.9	0.1	9.8	9.4	0.5	11.8	21.7	2.1
Myctophidae	0.6	0.3	0.1	4.1	4.4	0.2	7.2	11.1	1.3	2.4	2.8	0.4
Cottoidei	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.5	0.4	0.0	0.0	0.0
Macrouridae	0.6	0.3	0.5	0.0	0.0	0.0	0.9	0.8	1.1	8.3	4.9	9.4
Cyclopteridae	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.5	1.4	1.2	0.7	6.0
Pleuronectidae	0.0	0.0	0.0	2.0	1.5	6.0	0.2	0.2	0.9	2.4	1.4	4.7

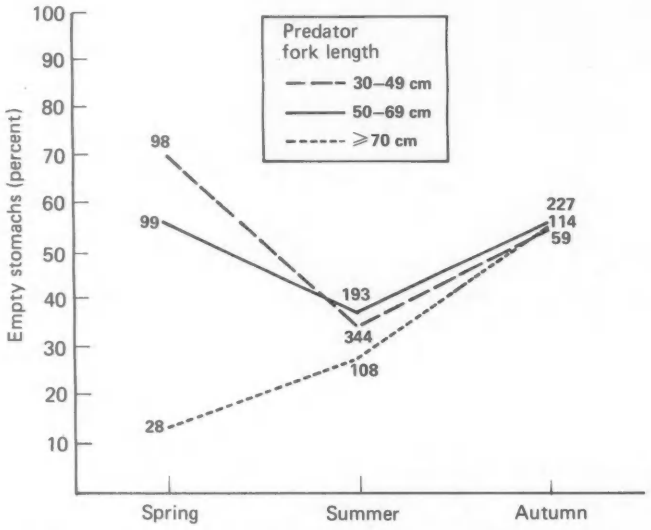

FIGURE 5.—Percent of empty stomachs by season and Greenland halibut size. (Numbers are sample sizes.)

stomach content weight of the fish 50–69 cm was also fairly constant although much less than in the larger fish. Although a midday drop in stomach content weight occurred in the two larger size groups, stomach content weight for the smallest size group appeared to steadily increase from 0100 h to 1200 h. The stomach content weight was highest but most variable in size group 30–49 cm during the 1500-1800 h time period.

Daily Ration

The mean stomach content weight and the daily ration varied among three size groups of Greenland halibut (Table 3). By percent body weight, the mean stomach content weight for 30–49 cm and 50–69 cm size groups were 1.4% and 1.3% respectively. Fish ⩾70 cm had the greatest mean stomach content weight (2.4% of body weight). Since gastric evacu-

TABLE 3.—Daily ration (*D.R.*) and mean stomach content weight (%BW ± SE) of Greenland halibut during each 3-h period. BW = body weight; *N* = No. of stomachs (including empty stomachs).

Size class (Temperature)	Time period	*N*	Mean stomach content weight (%BW ± SE)
30–49 cm	2400–0300	64	0.4700 ± 0.1772
(2.64°C)	0300–0600	21	0.9537 ± 0.4470
fish as prey	0600–0900	44	1.1542 ± 0.2926
a = 0.0143	0900–1200	59	1.7173 ± 0.3097
R = 0.0194	1200–1500	27	1.8937 ± 0.5661
D.R. = 0.6644	1500–1800	52	2.5844 ± 1.4731
	1800–2100	49	0.7300 ± 0.2425
squid as prey	2100–2400	34	1.9124 ± 0.3710
a = 0.0079			
R = 0.0107			$\bar{S}$ = 1.4270
D.R. = 0.3665			
50–69 cm	2400–0300	49	0.9141 ± 0.1306
(2.93°C)	0300–0600	78	1.5944 ± 0.3292
fish as prey	0600–0900	108	1.6596 ± 0.3011
a = 0.0143	0900–1200	70	1.0256 ± 0.2566
R = 0.0200	1200–1500	70	1.6406 ± 0.2736
D.R. = 0.6380	1500–1800	87	0.8967 ± 0.2340
	1800–2100	97	1.5372 ± 0.3077
squid as prey	2100–2400	111	1.3652 ± 0.2646
a = 0.0079			
R = 0.0111			$\bar{S}$ = 1.3292
D.R. = 0.3541			
⩾70 cm	2400–0300	25	2.8888 ± 0.6365
(2.96°C)	0300–0600	22	2.4635 ± 0.6325
fish as prey	0600–0900	28	3.2101 ± 0.6714
a = 0.0143	0900–1200	21	1.0156 ± 0.3308
R = 0.0201	1200–1500	40	2.8228 ± 0.5439
D.R. = 1.1712	1500–1800	40	1.7294 ± 0.4454
	1800–2100	41	2.5454 ± 0.6559
	2100–2400	33	2.7468 ± 0.4782
			$\bar{S}$ = 2.4272

ation rate (R) is affected by prey type, the constant a, used to calculate R for each size group, was determined by the percentage by weight of the main prey items (fish or squid). In size group 30–49 cm, where fish constituted 72% and squid constituted 25% by weight of the diet, both a = 0.0143 (fish as prey) and a = 0.0079 (squid as prey) were used for calculating R. For size group 50–69 cm, fish constituted 47% of the diet and squid 52%, so gastric evacuation rates were also calculated by using both a = 0.0143 and a = 0.0079. For size group ⩾70 cm, prey fish comprised 94% of the diet, and a = 0.0143 was used for calculating the gastric evacuation rate.

Large Greenland halibut (⩾70 cm) had the highest daily ration value (1.17%), measured as percentage of body weight per day (BWD), followed by the size group 30–49 cm (0.66% BWD). The 50–59 cm size group had the lowest daily ration value, 0.64% BWD

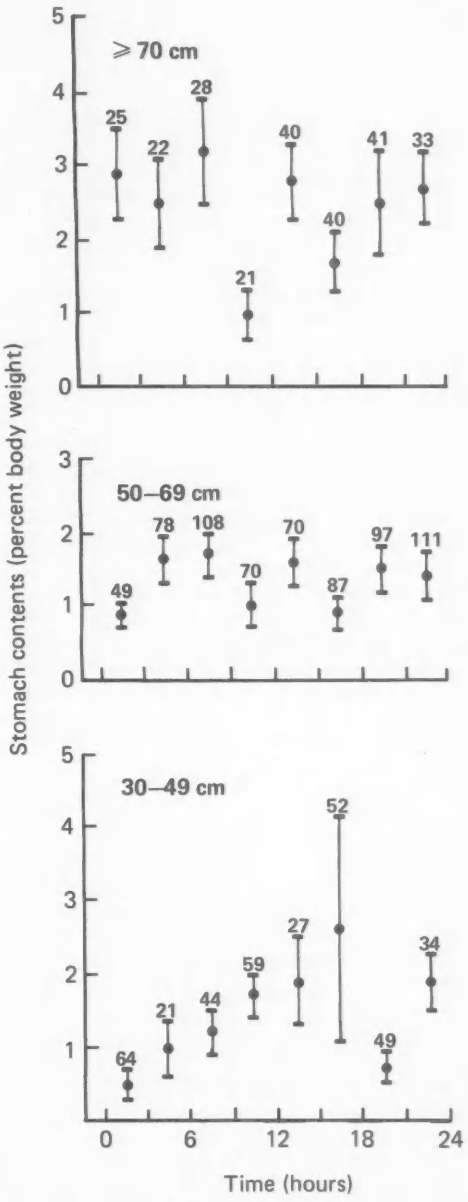

FIGURE 6.—Diel changes in mean stomach content weight (%BW ± SE) in the stomachs of three different size groups of Greenland halibut (the number above each bar was the sample size).

for fish prey and 0.35% BWD for squid prey. Since, fish and squid each constituted about one half of the stomach contents by weight in this size group, the actual daily ration lies within the range of the two values, 0.64% and 0.35%.

DISCUSSION

This study demonstrates size-dependent prey preference by Greenland halibut; halibut <20 cm fed primarily on euphausiids whereas those ≥20 cm were largely fish and squid eaters. It is not surprising to find that walleye pollock was the dominant prey (Table 1) of Greenland halibut because the estimated biomass of walleye pollock in the Bering Sea area is about 10,000,000 metric tons (Bakkala and Wespestad 1983). Livingston et al. (1985[5], 1986) noted that walleye pollock is a major food source not only for marine birds, marine mammals, and man, but also serves as a major food source for dominant components of the eastern Bering Sea groundfish complex. Other studies have also shown the importance of walleye pollock as food of Greenland halibut (Moiseev 1953; Mito 1974; Smith et al. 1978) in the eastern Bering Sea.

In this study, large Greenland halibut (≥70 cm) ate fish almost exclusively. Bowering and Lilly (1985) found that 65–69 cm was the length at which Greenland halibut in the northwestern Atlantic began to switch from smaller pelagic fish (*Mallotus villosus*) to larger groundfish (*Gadus morhua, Sebastes* sp., Anarhichadidae, Pleuronectidae, Zoarcidae) as food. Mikawa (1963) noted increased piscivory with size in Greenland halibut sampled in several areas of the North Pacific. Mito (1974) also showed the same trend; he found that 65–90 cm Greenland halibut ate 20–40 cm long walleye pollock. These observations suggest that large Greenland halibut (≥70 cm) feed on larger sized groundfish which may be lower in the water column whereas the smaller Greenland halibut (<70 cm) feed on smaller sized pelagic fish in the upper water column.

Shuntov (1970) and Mikawa (1963) noted seasonal depth migrations for Greenland halibut and interpreted the summer movement into shallower waters as a feeding migration related to migrations of walleye pollock. Based on the size distribution of walleye pollock in midwater trawl catches near the Pribilof Islands and westward over the Aleutian Basin, Livingston and Dwyer (1986) found that small (age 0) pollock occurred in near-slope and shelf areas, medium (age 1) pollock in shelf areas, while larger (>1 year old) pollock occurred in all areas during summer. Therefore, it can be concluded that in the slope area, where juvenile walleye pollock (age 0 and 1) of the appropriate size for smaller Greenland halibut were not available, the smaller sized (30–69 cm) Greenland halibut ate the available prey, cephalopods and deep-water fishes, while the larger ones (≥70 cm) consumed mostly larger walleye pollock (≥30 cm) and other fish regardless of depth or season.

No clear diel feeding trends were found. The lack of trends may be related to the large variations of the time of sunrise and sunset in different seasons in the Bering Sea. Other studies have varied findings. Mito (1974) reported that Greenland halibut fed primarily from sunset to midnight based on limited sample sizes (six specimens in some time periods). Shuntov (1970) showed that this species fed continuously in the Okhotsk Sea, although feeding was somewhat higher during the night. By comparing day and night catch rates, Chumakov (1969) concluded that Greenland halibut (in the Iceland area) made daily vertical migrations (staying close to the bottom during the day and moving up in the water column at night). However, he did not correlate this behavior with diel feeding. Thus, the literature and this study show no definite diel feeding trend in Greenland halibut.

Daily Ration

Daily ration calculations were based on the evacuation rate of one prey item (pollock or squid) using Elliott and Persson's (1978) model. Other authors (Durbin et al. 1983; Dwyer 1984) have calculated total daily ration by adding up the separate daily rations of the different prey items. Persson (1984) demonstrated that the evacuation of a specific food item can be dependent on the ingestion of other food items. Therefore, it may be erroneous to apply the food consumption model to estimate the consumption of individual prey types separately. Persson (1984) suggested that the only practical solution to calculate the daily rations of different prey items is to calculate the mean weight of each food item remaining in the digestive tract over 24 hours and multiply the fraction it constitutes of the total mean content with the total daily ration. This is necessary

[5]Livingston, P. A., M. S. Yang, and D. Wencker. 1985. The importance of juvenile pollock in the diet of key fish species in the eastern Bering Sea. Unpubl. manuscr., 19 p. Presented as the workshop on comparative biology, assessment, and management of gadoids from the North Pacific and Atlantic Oceans, 24–28 June 1985. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98115.

since the complexity of feeding and evacuation patterns in field populations of fish makes it impossible to estimate the consumption and evacuation of different food items ingested at different times.

Bowering and Lilly (1985) estimated the consumption rate of capelin, *Mallotus villosus*, by Greenland halibut in the northwestern Atlantic, using estimates of gastric evacuation rate for Atlantic cod, *Gadus morhua*, on capelin from Minet and Perodou's (1978) study. Assuming a linear gastric evacuation model, they found the time for Greenland halibut to complete digestion of capelin at 2°–3°C was 3–5 days. By using the gastric evacuation rate calculated from this study, the time needed by large Greenland halibut (≥70 cm) to evacuate 99% of a pollock meal at 3°C was 4.2 days, a value very similar to Bowering and Lilly's (1985) estimate.

Livingston and Dwyer (1986[6]) calculated an average daily ration for arrowtooth flounder of 0.62% of body weight per day. This value is close to the daily ration values calculated from this study. Since Greenland halibut and arrowtooth flounder are ecologically and morphologically similar species, it is not surprising to find their daily ration needs are similar.

Huebner and Langton (1982) performed a gastric evacuation study on winter flounder, *Pseudopleuronectes americanus*. They used squid as food for fish 10–40 cm at 5.5°–7.0°C to get a gastric evacuation rate of 0.079/h and calculated daily ration in the range of 1.8–2.4% BWD. Compared to these values, the daily ration of Greenland halibut calculated in this study is low, possibly due to the lower temperatures in this study.

Greenland halibut ≥70 cm apparently ate a higher daily ration (1.17% of body weight per day) than did those <70 cm (0.66% and 0.64% BWD for size group 30–49 cm and 50–69 cm, respectively). Flowerdew and Grove (1979) studied the effects of body weight and meal size on gastric emptying time in the turbot, *Scophthalmus maximus*. Their results showed that large fish emptied a meal of a given size from the stomach at a faster rate than small fish, and large meals in a given fish were processed at faster rate than small meals. Dwyer (1984) also found a higher daily ration value for larger walleye pollock in the eastern Bering Sea. However, Windell (1978) stated that small fish generally consume proportionately more food per unit weight, and some studies showed this trend; Daan (1973) used a prey size dependent evacuation model and found that ration decreased with increasing fish size for North Sea Atlantic cod. Huebner and Langton (1982) calculated daily ration of winter flounder and found the largest fish (>300 g) had the smallest ration. Other studies (Elliott 1972; Hofer et al. 1982) showed that predator size and meal size have little or no effects on gastric evacuation rate. Durbin and Durbin (1980) concluded from an extensive review of daily ration studies that particle size and meal size relationships on gastric evacuation rates deserve further study. Since the ≥70 cm Greenland halibut in this study, which had the highest daily ration, also consumed much larger walleye pollock than the other predator size groups, a particle size interaction with gastric evacuation rate seems a likely avenue for further research.

[6]Livingston, P. A., and D. A. Dwyer. 1986. Food web interactions of key predatory fish with northern fur seal, *Callorhinus ursinus*, in the eastern Bering Sea during summer 1985. *In* T. R. Loughlin and P. A. Livingston (editors), Summary of joint research on the diets of northern fur seals and fish in the Bering Sea during 1985, p. 57–92. NWAFC 86-19. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

ACKNOWLEDGMENTS

We are grateful to Sandra Noel, Karen Conlan, and Wendy Carlson for their excellent work on the figures. Thanks also go to Doug Milward and Geoff Lang for their assistance on the stomach content analyses. We also want to thank the two reviewers for their comments on the earlier manuscript.

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ASPECTS OF THE BIOLOGY OF TWO SCYLIORHINID SHARKS, *APRISTURUS BRUNNEUS* AND *PARMATURUS XANIURUS*, FROM THE UPPER CONTINENTAL SLOPE OFF SOUTHERN CALIFORNIA

JEFFREY N. CROSS[1]

ABSTRACT

The distribution, abundance, reproductive cycle, and food habits of two scyliorhinid sharks are discussed. Catsharks occurred on 87% of 71 longline sets and in 6% of 48 trawls. Longline catches were stratified by habitat into banks (hard substrate) and mud (soft substrate). *Apristurus brunneus* occurred more frequently on mud sets than on bank sets, but its abundance was similar in both habitats. *Parmaturus xaniurus* occurred equally frequently on mud and bank sets, but it was more abundant on bank sets. Catches of both species consisted of adults and adolescents; juveniles were rare or absent. Historical collections suggest that juveniles are mesopelagic.

Male *P. xaniurus* matured at a smaller size than male *A. brunneus*. Females of both species matured at about the same size and fecundity increased with female size. The proportion of body weight devoted to gonads and maximum oocyte size were greater among *P. xaniurus*, but fecundity and the proportion of females carrying egg cases were greater among *A. brunneus*. Seasonal changes in gonadal development were not well defined for either species. Members of both populations may have been reproductively active throughout the year.

The diets of both species comprised, in order of importance, crustaceans, teleosts, and squids. Most prey consumed were pelagic; however, it is not known where in the water column the catsharks obtained their prey.

The Scyliorhinidae is the largest family of living sharks with about 94 valid species (Nelson 1984). Commonly known as catsharks, they occur worldwide from tropical to cold-temperate and arctic waters from the intertidal to depths greater than 2,000 m. Little is known about the biology of most scyliorhinid sharks despite their abundance and widespread distribution (Springer 1979; Compagno 1984).

Apristurus brunneus Gilbert, the brown catshark, occurs in the eastern Pacific Ocean from northern British Columbia, Canada, to northern Baja California, Mexico, and perhaps south to Central America and Peru. It is common on the outer continental shelf and upper slope off British Columbia, Washington, and northern California (Springer 1979) but is considered uncommon off central and southern California (Miller and Lea 1972). DeLacy and Chapman (1935) and Cox (1963) described its egg case. Jones and Geen (1977) made observations on its distribution, reproduction, and food habits in British Columbia waters.

Parmaturus xaniurus Gilbert, the filetail catshark, occurs in the eastern Pacific Ocean from central California to the Gulf of California, Mexico. It is fairly common on the outer continental shelf and upper slope (Compagno 1984). Cox (1963) described its egg case. Lee (1969) reported that juveniles were captured by midwater nets in the Santa Barbara basin off southern California. Springer (1979) reported that *P. xaniurus* were observed eating moribund lanternfishes (Myctophidae) at the bottom of the oxygen-poor Santa Barbara Basin.

The objective of this study was to increase the knowledge of the life histories of *A. brunneus* and *P. xaniurus* by analyzing data on the distribution, abundance, reproduction, and food habits of these species collected during a survey of the fishes of the upper continental slope off southern California (Cross 1987).

MATERIALS AND METHODS

Fishes occurring on or near the bottom between 290 and 625 m were collected by otter trawl and longline. Forty-eight trawls were made between November 1981 and August 1983 (Fig. 1). A single warp semiballoon trawl with 7.6 m headrope, 8.8 m

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Manuscript accepted June 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

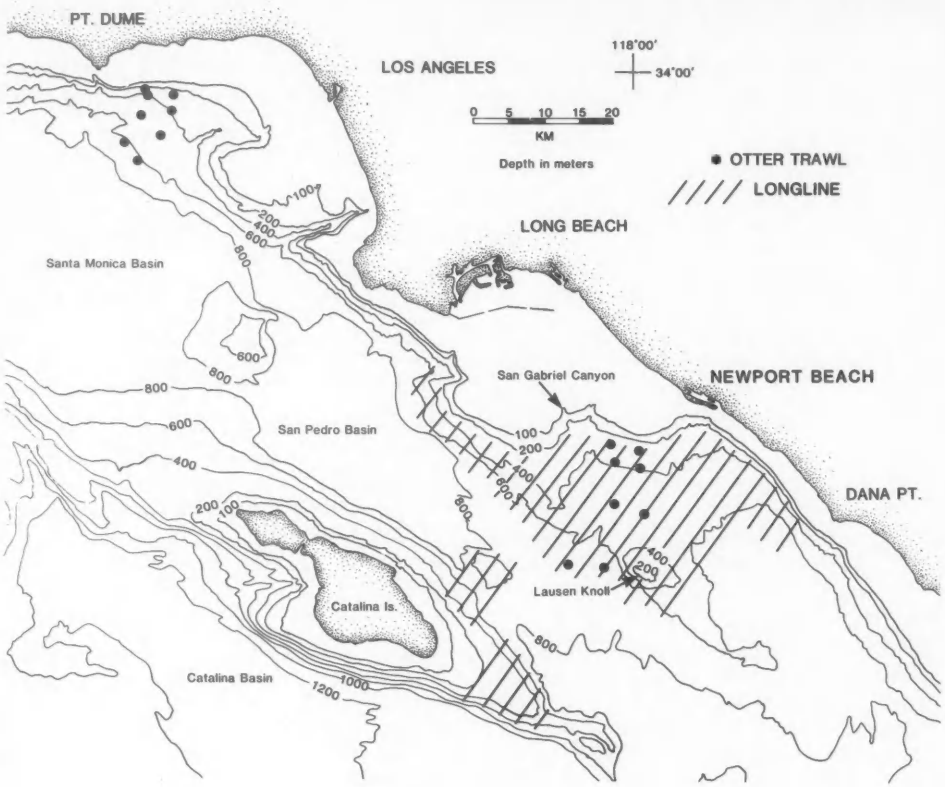

FIGURE 1.—Map of the study area.

footrope, 4.1 cm (stretched) body mesh, and 1.3 cm (stretched) cod end liner was towed along an isobath at approximately 2.5 knots for 10 minutes.

Seventy-one trips were made with commercial longline fishermen between June 1983 and November 1984 (Fig. 1). A unit (tub) of longline gear consisted of about 650 m of groundline bearing approximately 600 hooks (4/0 and 5/0 standard rockcod) on short leaders. Salted pieces of *Engraulis mordax* and, to a lesser extent, *Scomber japonicus* were used as bait. Three to six tubs tied together formed a set. Usually, lines were set between the hours of 1000 and 1400 and retrieved the following day between 0600 and 1000.

Sinking and floating longlines were set. On sinking sets, weights (bricks) were tied to either end of the groundline and at intervals along the line. On floating sets, weights and floats (soda bottles) were tied alternately to groundline; the distance between two weights encompassed 50–60 hooks. Anchors and buoy lines were attached to each end of the groundline. Floating and sinking lines were set on mud, but only floating lines were set on banks. Sets on the mud ranged from 400 to 600 m deep; sets on the banks ranged from 350 to 550 m deep.

Scyliorhinid sharks were taken to the laboratory where they were measured to the nearest 1 mm total length (TL) and weighed to the nearest 0.1 g. The left clasper of males was measured to the nearest 0.5 mm. The gonads were removed and weighed to the nearest 0.1 g. All eggs larger than 4 mm in diameter were separated from the ovary and measured to the nearest 1 mm. Stomachs were removed and placed in 10% buffered formalin; the contents were

washed in water, sorted, and identified to the lowest taxon practicable; pieces of bait were ignored.

Size at sexual maturity was estimated for males by change in relative size of the claspers and testes, and for females by change in relative size of the ovaries and presence of egg cases in the oviducts (Pratt 1979). Polynomial regressions were fit to the data for males (SAS 1982). The reproductive season was determined by enlarged testes in the males and the presence of full-sized eggs in the ovaries of the females. The gonadosomatic index (GSI) was calculated for the sexes of both species from

$$\text{GSI} = (\text{gonad weight/body weight}) \times 100.$$

Analyses of stomach data were summarized by the index of relative importance (IRI) modified from Pinkas et al. (1971):

$$\text{IRI} = PO(PN + PW)$$

where PO is percent occurrence, PN is percent numbers, and PW is percent weight calculated for each prey category. The length of intact prey was measured.

Catch/effort data (where a unit of effort was one tub of line) were transformed to $\log_{10}$ and analyzed for habitat, season, and depth differences by analysis of covariance (ANCOVA) for unbalanced designs (SAS 1982) with habitat and season as the main effects and depth as the covariate. Catch per tub for each positive set was determined by averaging the catches of the constituent tubs.

Fish size data were analyzed for habitat, season, and depth differences by ANCOVA for unbalanced designs. The data were not transformed because size was approximately normally distributed.

Geometric mean weight-length regressions were calculated from the logarithmic transformation of

$$W = aL^b$$

where W is weight in grams, L is total length in millimeters, and a and b are fitted constants (Ricker 1973). The regression coefficients (b) were compared by the method of Clarke (1980).

The sediments of the upper continenal slope off Newport Beach are predominantly green silty clays. Sand content is fairly constant down slope (mean = 12% by dry weight); areas around the offshore banks and the shoulders of the submarine canyons are sandier (25–50% by dry weight). Organic content increases from 5 to 7% (as total volatile solids) at 290 m to 11–14% at 625 m (SCCWRP 1983[2]). Between 600 and 700 m, the slope gives way to the low-oxygen San Pedro Basin to the northwest and to the deeper San Diego Trough to the southeast (Fig. 1).

Longline fishermen recognize two habitats on the slope: hard substrate banks and soft, relatively featureless (on a fathometer) mud bottom. Surface sediments on the banks are a mixture of coarse sand, shell hash, and occasional rocks. As used herein, banks include submerged mountains, shoulders of submarine canyons, and isolated mounds as small as a few hundred meters across and 20–30 m high. The mud bottom is green silty clay and is the predominant habitat on the slope.

Oceanographic measurements in the water column off Newport Beach showed weak and decreasing gradients with increasing depth. The mean annual temperature was 8.3°C (SD = 0.3, N = 64, min = 7.5, max = 9.1) at 300 m and 6.5°C (SD = 0.2, N = 25, min = 6.0, max = 6.9) at 500 m. Mean annual dissolved oxygen was 1.21 ppm (SD = 0.26, N = 54, min = 0.76, max = 1.94) at 300 m and 0.48 ppm (SD = 0.10, N = 20, min = 0.31, max = 0.72) at 500 m. Some of the variation at 300 m was the result of seasonal changes related to upwelling. In the spring, temperature and dissolved oxygen decreased, and salinity and density increased (SCCWRP fn. 2).

RESULTS

Distribution and Abundance

The occurrence of scyliorhinid sharks in trawl catches was markedly different from longline catches. Catsharks were caught in 3 (6%) of the 48 otter trawls. The six individuals collected accounted for <0.1% of all fish caught in trawls. Catsharks were caught on 62 (87%) of the 71 longline sets (212 tubs of gear examined). The 698 individuals collected accounted for 5.8% of the fish caught (2.8% of catch weight) on longlines.

Apristurus brunneus were caught on 50 (70%) sets; 475 individuals were collected. *Parmaturus xaniurus* were caught on 53 (75%) sets; 223 individuals were collected. The two species occurred independently on the tubs of longline gear (χ^2 = 0.39, $P > 0.05$). They were equally abundant on bank

[2]SCCWRP. 1983. A survey of the slope off Orange County, California. Report to County Sanitation Districts of Orange County. Long Beach: Southern California Coastal Water Research Project, 208 p.

sets ($t = 0.56$, $P > 0.05$), but *A. brunneus* were more abundant than *P. xaniurus* on mud sets ($t = 3.50$, $P < 0.01$) (Table 1).

Apristurus brunneus occurred on 61% of the bank sets and 79% of the mud sets. Catches were not significantly different among habitats, seasons, or depths (ANCOVA, $P > 0.05$). Mean catch per tub in the mud habitat was not significantly different between floating and sinking sets ($t = 1.35$, $P = 0.19$).

Parmaturus xaniurus occurred on 73% of the bank sets and 76% of the mud sets. Catches were significantly higher on bank sets than on mud sets (ANCOVA, $P < 0.05$). Catches were nearly twice as high on bank sets in the winter compared with bank sets in the summer. Catch increased with increasing depth on banks, but it decreased with increasing depth on mud. Catches on the mud were not significantly different between floating and sinking sets ($t = 0.76$, $P = 0.45$.).

Size

There were no significant differences in the regression coefficients of the weight-length relationships between males and females of either *A. brunneus* or *P. xaniurus* over the range of sizes examined (Table 2; Fig. 2). There were no significant differences in the size of *A. brunneus* or *P. xaniurus* among habitats, seasons, or depths (ANCOVA, $P > 0.05$).

TABLE 1.—Catch statistics for *Apristurus brunneus* and *Parmaturus xaniurus* from longline collections on banks and mud. No. = number, wt = weight in kg, N = number of positive sets, $\bar{X}$ = mean, SD = one standard deviation.

		Banks			Mud		
Species		N	$\bar{X}$	SD	N	$\bar{X}$	SD
A. brunneus	No./tub	20	2.3	2.1	30	3.7	4.6
	Wt/tub	20	0.9	0.8	30	1.5	1.8
P. xaniurus	No./tub	24	2.0	2.0	29	1.1	1.1
	Wt/tub	24	0.6	0.6	29	0.4	0.4

Reproduction

Based on relative change in clasper length and gonad weight, *A. brunneus* males reached sexual maturity between 450 and 500 mm TL; *P. xaniurus* males reached sexual maturity between 375 and 425 mm TL (Fig. 3). Females of both species reached sexual maturity between 425 and 475 mm TL (Fig. 4). Only the right ovary was functional in both species.

Seasonal changes in gonadal development were not pronounced among *A. brunneus*. Male and female GSIs were highest in winter and lowest in summer (Fig. 5). Large oocytes were present in the right ovary of females throughout the year (Fig. 6).

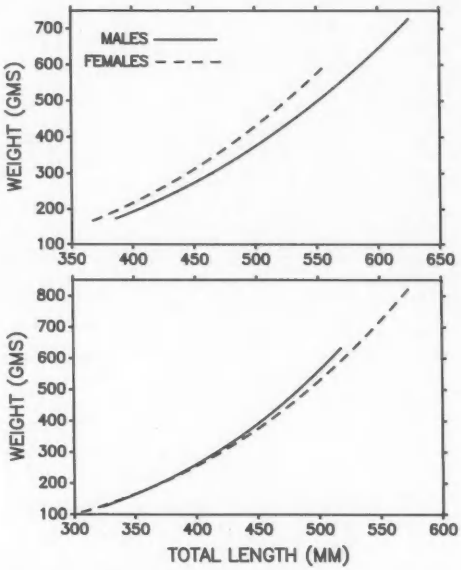

FIGURE 2.—Weight-length relationships of *Apristurus brunneus* (above) and *Parmaturus xaniurus* (below).

TABLE 2.—Geometric mean weight-length regressions for *Apristurus brunneus* and *Parmaturus xaniurus*. N = sample size, min = minimum total length (TL) in mm, max = maximum TL, W = body weight in g, L = TL, $L1$ = lower 95% confidence interval for b, $L2$ = upper 95% confidence interval, r = correlation coefficient.

Species	Sex	N	min	max	$W = aL^b$	$L1$	$L2$	r
A. brunneus	F	149	369	556	$W = 2.379 \times 10^{-6} L^{3.059}$	2.839	3.279	0.899
	M	90	389	625	$W = 3.577 \times 10^{-6} L^{2.971}$	2.809	3.134	0.966
P. xaniurus	F	76	307	574	$W = 9.377 \times 10^{-7} L^{3.242}$	3.045	3.439	0.965
	M	89	325	516	$W = 3.163 \times 10^{-7} L^{3.427}$	3.166	3.688	0.934

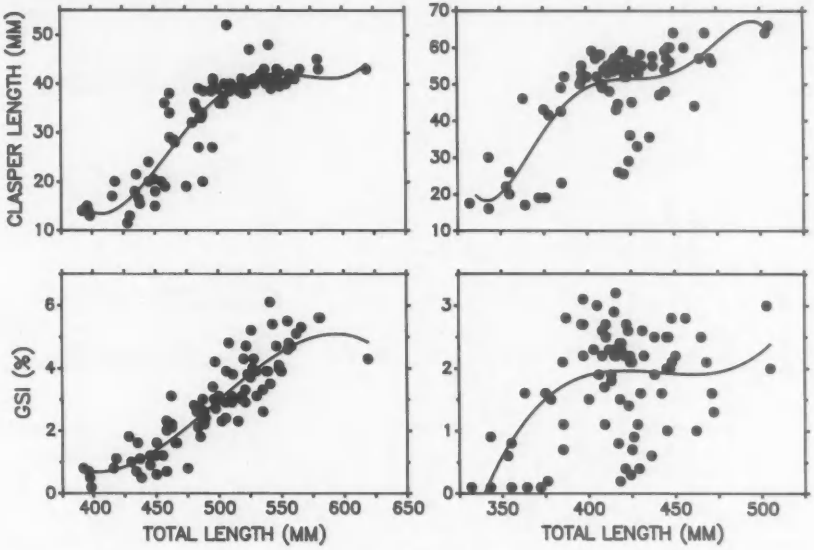

FIGURE 3.—Left clasper length and gonadosomatic index (GSI) versus total length of male *Apristurus brunneus* (left) and *Parmaturus xaniurus* (right).

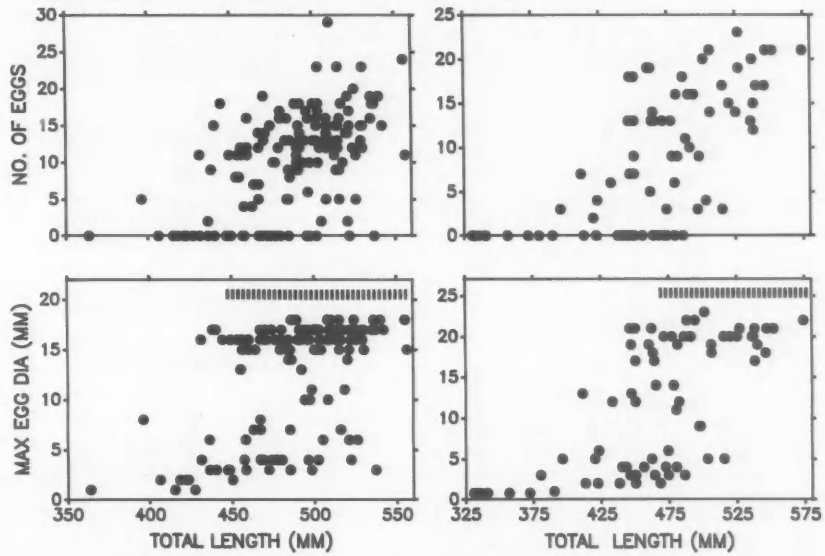

FIGURE 4.—Number of oocytes (>4 mm) and maximum oocyte diameter versus total length of female *Apristurus brunneus* (left) and *Parmaturus xaniurus* (right). Cross-hatched bar indicates size of fish carrying egg cases.

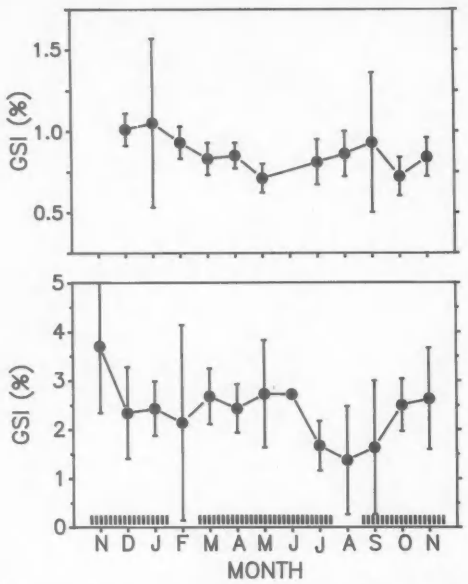

FIGURE 5.—Mean gonadosomatic index (GSI) of *Apristurus brunneus* males (above) and females (below) from November 1983 through November 1984. Cross-hatched bar indicates months when females were carrying egg cases. Vertical bars are 95% confidence intervals.

The number of oocytes larger than 4 mm was correlated with size among mature females ($r = 0.425$, $P < 0.001$); the maximum number was 29. Atretic oocytes were observed from March through November and spent fish (no oocytes larger than 2–3 mm; $N = 2$) were collected in December and July.

Egg cases were found in the oviducts of 48 *A. brunneus* females larger than 450 mm (37% of mature females); the egg cases were not completely formed in only one individual. Females with egg cases were collected every month except February and August (Fig. 5). More mature females carried egg cases from December through May (42%) than from June through November (29%), although the difference was not significant ($\chi^2 = 2.24$, $P > 0.1$). Egg case length (measured between the tendrils) was correlated with female total length ($r = 0.386$, $P < 0.02$). The mean ratio of egg case length to female total length was 0.114 (SD = 0.019).

Seasonal changes in gonadal development were not pronounced among *P. xaniurus*. Male GSI was high throughout the year; female GSI was highest in winter and lowest in summer (Fig. 7). Large

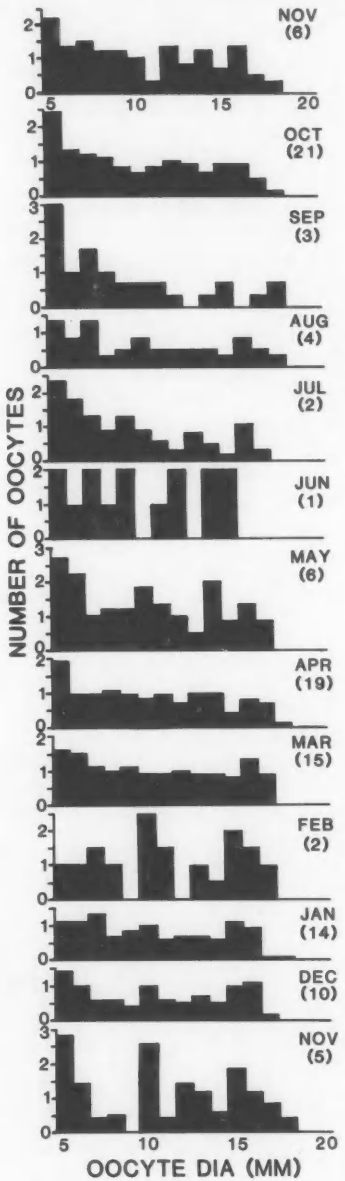

FIGURE 6.—Mean monthly oocyte (>4 mm) size-frequency distribution of *Apristurus brunneus* from November 1983 (bottom) to November 1984 (top). Sample size in parentheses.

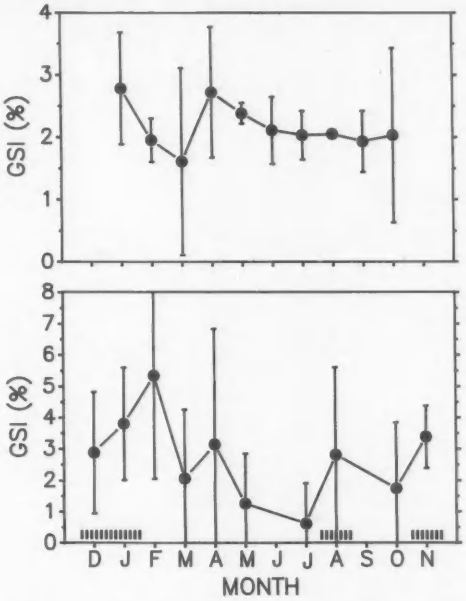

FIGURE 7.—Mean gonadosomatic index (GSI) of *Parmaturus xaniurus* males (above) and females (below) from December 1983 through November 1984. Cross-hatched bar indicates months when females were carrying egg cases. Vertical bars are 95% confidence intervals.

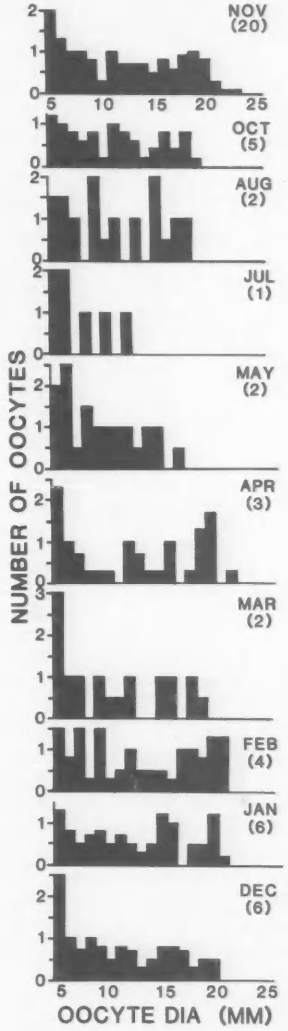

FIGURE 8.—Mean monthly oocyte (>4 mm) size-frequency distribution of *Parmaturus xaniurus* from December 1983 (bottom) to November 1984 (top). Sample size in parentheses.

oocytes were present in the right ovary of females every month except July (Fig. 8). The number of oocytes larger than 4 mm was correlated with size among mature females ($r = 0.597$, $P < 0.001$); the maximum number was 23. Atretic oocytes were observed in May, August, and November and spent fish (no oocytes larger than 3–4 mm; $N = 3$) were collected in January and March.

Egg cases were present in the oviducts of five *P. xaniurus* females larger than 470 mm (10% of mature females); the egg cases were not completely formed in one individual. One 450 mm TL female had recently released two egg cases as evidenced by distended oviducts. Egg cases were present in females collected in December, January, August, and November (Fig. 7). The mean ratio of egg case length to female total length was 0.156 (SD = 0.023).

Food Habits

Stomachs from 211 *A. brunneus* were examined; 138 (65%) were empty or contained only traces of well-digested prey. There was no seasonal trend in the proportion of empty stomachs. Crustaceans, teleosts, and molluscs constituted the diets of the remaining individuals (Table 3). Natantian decapods

TABLE 3.—Stomach contents of 73 *Apristurus brunneus* (mean size = 496 mm TL, SD = 40, min = 396, max = 619). *PO* = percent occurrence, *PN* = percent number, *PW* = percent weight, IRI = index of relative importance.

	PO	*PN*	*PW*	IRI
Crustacea	97.3	74.2	67.3	13,768
Isopoda	9.6	3.0	0.8	36
Epicaridea	9.6	3.0	0.8	36
Mysidacea	1.4	0.5	0.4	1
Euphausiacea	6.8	4.5	4.5	61
Decapoda	71.2	61.8	58.4	8,558
Natantia	61.6	52.7	48.9	6,259
Penaeidea	13.7	7.5	6.6	193
Sergestidae	12.3	5.6	4.7	127
Sergestes similis	11.0	4.9	3.9	97
Petalidium suspiriosum	1.4	0.7	0.8	2
Penaeidae	2.7	1.9	1.8	10
Bentheogennema sp.	2.7	1.9	1.8	10
Caridea	45.2	23.7	28.8	2,373
Pasiphaeidae	45.2	23.7	28.8	2,373
Pasiphaea sp.	27.4	14.0	16.3	830
Pasiphaea pacifica	13.7	5.1	8.3	184
Pasiphaea emarginata	1.4	1.4	1.4	4
Reptantia	15.1	6.6	7.8	217
Anomura	15.1	6.6	7.8	217
Galatheidae	15.1	6.6	7.8	217
Pleuroncodes planipes	5.5	1.9	2.0	21
Mollusca	20.5	8.4	11.4	406
Pelecypoda	1.4	0.3	0.1	<1
Cephalopoda	19.2	8.0	11.2	369
Coleoidea	19.2	8.0	11.2	369
Decapoda	19.2	8.0	11.2	369
Teuthoidea	19.2	8.0	11.2	369
Gonatus sp.	4.1	2.5	3.3	24
Abraliopsis felis	2.7	0.8	1.0	5
Loligo opalescens	1.4	0.5	0.8	2
Osteichthyes	42.5	16.6	21.0	1,598
Myctophidae	6.8	3.8	4.4	56

(40% of total IRI), especially carideans of the family Pasiphaeidae (15%), dominated the contents. Teleosts (10%), including myctophids, were also important. Most fish remains in the stomachs were digested beyond recognition. Squids made up the remainder of the diets (3%). There was no evidence for a size-related change in diet; the dominant prey occurred in all sizes of fish examined.

The stomachs of 73 *A. brunneus* contained an average of 2.7 prey items (SD = 1.7, max = 10) and the contents averaged 0.7% of body weight (SD = 0.4, max = 1.99). Content weight was not correlated with body weight (Spearman $r_s = 0.227$, $P > 0.2$), and carapace length of the most frequently occurring prey, *Pasiphaea* spp., was not correlated with fish size ($r_s = -0.168$, $N = 33$, $P > 0.2$). Relative content weight was not significantly different among months (Kruskal-Wallis test, $H = 14.89$, $P = 0.19$).

Stomachs from 155 *P. xaniurus* were examined; 85 (55%) were empty or contained only traces of well-digested prey. There was no seasonal trend in the proportion of empty stomachs. Crustaceans, teleosts, and molluscs constituted the diets of the remaining individuals (Table 4). Reptantian decapods (36% of total IRI), particularly the galatheid *Pleuroncodes planipes* (12%), dominated the contents. Natantian decapods (3%) and teleosts (7%), including myctophids, were also important. Most fish remains in the stomach were digested beyond recognition. Squids made up a small part of the diets (<1%). There was no evidence for a size-related change in diet; the dominant prey occurred in all sizes of fish examined.

The stomachs of 70 *Parmaturus xaniurus* contained an average of 2.4 prey items (SD = 1.3, max = 5) and the contents averaged 1.2% of body weight (SD = 0.9, max = 4.7). Content weight was correlated with body weight (Spearman $r_s = 0.372$, $P < 0.002$). Relative content weight was not significantly different among months (Kruskal-Wallis test, $H = 13.26$, $P = 0.35$).

TABLE 4.—Stomach contents of 70 *Parmaturus xaniurus* (mean size = 438 mm TL, SD = 47, min = 341, max = 547). *PO* = percent occurrence, *PN* = percent number, *PW* = percent weight, IRI = index of relative importance.

	PO	*PN*	*PW*	IRI
Crustacea	97.1	75.5	72.1	14,332
Isopoda	4.3	1.6	0.5	9
Epicaridea	4.3	1.6	0.5	9
Bopyridae	2.9	1.0	0.3	4
Munidon parvum	2.9	1.0	0.3	4
Euphausiacea	24.3	8.6	5.4	340
Decapoda	81.4	56.5	59.2	9,421
Natantia	21.4	10.8	11.9	486
Penaeidea	11.4	4.6	4.0	98
Sergestidae	11.4	4.6	4.0	98
Sergestes similis	11.4	4.6	4.0	98
Caridea	12.9	5.0	7.0	155
Pasiphaeidae	12.9	5.0	7.0	155
Pasiphaea pacifica	10.0	4.0	5.8	98
Reptantia	67.1	38.5	43.4	5,495
Anomura	65.7	38.2	43.0	5,335
Galatheidae	65.7	38.2	43.0	5,335
Pleuroncodes planipes	40.0	21.9	26.1	1,920
Brachyura	1.4	0.4	0.4	1
Mollusca	5.7	1.4	1.8	18
Cephalopoda	5.7	1.4	1.8	18
Coleoidea	5.7	1.4	1.8	18
Decapoda	5.7	1.4	1.8	18
Teuthoidea	5.7	1.4	1.8	18
Osteichthyes	48.6	20.8	25.3	1,036
Myctophidae	10.0	4.8	6.1	109

DISCUSSION

Distribution and Abundance

Apristurus brunneus and *Parmaturus xaniurus* were a common, though unwanted, part of the longline catch on the upper continental slope off southern California. The abundance of both species was underestimated by trawl. Among the 29 species (12,074 individuals) caught on longlines, *A. brunneus* ranked 7th in abundance and *P. xaniurus* ranked 10th. They ranked 29th and 34th, respectively, among the 42 species (7,264 individuals) taken in trawls (Cross 1987). The bias of small trawls against large demersal fishes is well known (Day and Pearcy 1968; Haedrich et al. 1975). Most previous fish collections on the slope off southern California were taken with small trawls which explains why these sharks are not considered common.

Catches of *A. brunneus* and *P. xaniurus* were similar on bank sets, but *A. brunneus* was more abundant on mud sets. The two species occurred independently at the scale of one tub of longline gear (about 650 m). *Apristurus brunneus* was equally abundant on mud and bank sets, and seasonal differences in distribution and catch were not apparent. *Parmaturus xaniurus* was more abundant on bank sets than on mud sets, suggesting some habitat selection. Catches of *P. xaniurus* were highest on banks in the winter; the reason for this is not known.

Juvenile *A. brunneus* and *P. xaniurus* were conspicuously absent from longline and trawl collections on the slope. Catsharks are generally regarded as demersal fishes (Compagno 1984), but *A. brunneus* and *P. xaniurus* have been captured in the water column. An undisclosed number of *A. brunneus* larger than 260 mm (TL assumed) were collected up to 172 m above the bottom in 373 m of water off British Columbia, Canada (Jones and Geen 1977). Sixty-nine *P. xaniurus* (99–320 mm) were collected in 43 midwater trawls from 9 to 490 m above the bottom in 527–582 m of water in the Santa Barbara Basin, CA (Lee 1969). The livers of *P. xaniurus* contain a high proportion of squalene, a low specific gravity oil that aids in hydrostatic balance (Springer 1979).

Juveniles and adolescents of both species were taken in midwater trawls in the Santa Barbara Basin (bottom depths between 490 and 576 m) (UCSB[3]). Catsharks occurred in 31 (41%) of 75 mid-

[3]UCSB. Collections taken by the University of California, Santa Barbara, with an opening and closing net between 1965 and 1967 and deposited in the Los Angeles County Museum of Natural History.

water trawls; 83% of the individuals were collected within 250 m of the bottom. Fifty-four *A. brunneus* (99–380 mm TL, median = 177) were collected in 22 trawls and 23 *P. xaniurus* (110–229 mm TL, median = 175) were collected in 17 trawls.

The occurrence of juveniles and adolescents of both species in midwater collections suggests that the water column, especially within 200–300 m of the bottom, is their nursery area, and would explain their conspicuous absence in benthic collections during the present study. Cailliet[4] also concluded that *P. xaniurus* are mesopelagic as juveniles and demersal as adults.

Interestingly, 119 midwater trawls in the Santa Cruz Basin, CA and near Rodriguez Seamount (most bottom depths between 1,200 and 2,200 m) (UCSB fn 3) captured no scyliorhinid sharks (the trawls were taken concomitantly with trawls in the nearby Santa Barbara Basin). Bottom depths >1,000 m may be beyond the range of both species. The deepest recorded collection of *A. brunneus* off southern California was 933 m (Roedel 1951); the deepest recorded collection of *P. xaniurus* was 687 m (Springer 1979). The absence of both species in midwater trawls in the Santa Cruz Basin and near Rodriguez Seamount would not be surprising if juveniles do not travel far horizontally and adults do not occur below 1,000 m.

Size

The largest *A. brunneus* collected during the present study (625 mm TL male) was less than the maximum recorded size (680 mm TL; Compagno 1984). The largest *P. xaniurus* (574 mm TL female) was greater than the maximum recorded size (550 mm TL; Compagno 1984). Weight-length relationships of males and females of both species were similar. It is not known if males and females that were the same size were the same age. Attempts at determining the ages of *P. xaniurus* were unsuccessful (Cailliet 1986[5]).

Reproduction

Like many scyliorhinid sharks, *A. brunneus* and *P. xaniurus* exhibit single oviparity: one fertilized egg enters each oviduct and, after a short period, is deposited in a tough egg case on the substrate where it is anchored by tendrils (Nakaya 1975). Embryonic development takes place largely outside the mother and may require a year to produce a hatchling (Compagno 1984).

Size at sexual maturity estimated during the present study agrees with published observations for both species (Jones and Geen 1977; Compagno 1984). Male *P. xaniurus* matured at a smaller size than male *A. brunneus*. Females of both species matured at about the same size and fecundity increased with female size. Fecundity was greater among *A. brunneus* as was the proportion of mature females carrying egg cases, but the proportion of body weight devoted to gonads and maximum oocyte size were greater among *P. xaniurus*.

Seasonal changes in gonadal development were not well defined for either species; individuals in both populations may be sexually active at any time of the year. Several observations suggest that oocyte production was seasonal: the highest proportion of adult females with oocytes <10 mm in diameter and the highest frequency of atretic oocytes were observed from summer through fall when GSI was lowest.

There are few published observations on reproductive cycles of scyliorhinid sharks. *Scyliorhinus canicula*, an abundant shelf and upper slope catshark in the northeastern Atlantic Ocean, lays eggs throughout the year. Seasonal maxima in egg capsule production are apparent, but timing varies with latitude. Size at sexual maturity also varies with latitude; fish mature at a larger size at higher latitudes (Ford 1921; Capapé 1977). The fecundity of female *S. canicula* (46–50 cm TL) ranges from 23 to 34 eggs; fecundity increases with fish size. Eggs are 16 mm in diameter at ovulation. Annual fecundity is about 96–115 eggs. In the Mediterranean Sea, egg capsule incubation times range from 180 days for eggs deposited during the summer to 285 days for eggs deposited during the winter (Capapé 1977).

Food Habits

Apristurus brunneus and *Parmaturus xaniurus* consumed, in order of importance, crustaceans, teleosts, and squids. Similar diets were reported for both species by Jones and Geen (1977), Cailliet (1981, see fn. 4), and Compagno (1984). The diets of the two catsharks were broadly similar except for the occurrence of crustaceans. Reptantian decapods

[4]Cailliet, G. M. 1981. Ontogenetic changes in the depth distribution and feeding habits of two deep-dwelling demersal fishes off California: sablefish and filetail cat sharks. [Abstr.] Am. Soc. Ichthyol. Herpetol. Sixty-first Annu. Meeting, Corvallis, OR.

[5]G. M. Cailliet, Moss Landing Marine Laboratories, Moss Landing, CA, pers. commun. July 1986.

dominated the diet of *A. brunneus* (36% of total IRI) while natantian decapods dominated the diet of *P. xaniurus* (40% of total IRI). This may be a result of habitat differences between the catsharks rather than prey selection. The epicaridean isopods in the stomach contents are crustacean parasites, and were probably ingested with their hosts.

A very high percentage of *A. brunneus* and *P. xaniurus* stomachs was empty. This may not be representative of their respective populations. Sharks caught by baited hooks have a higher proportion of empty stomachs, and lower stomach content weight, than sharks caught by gill net (Medved et al. 1985).

Most of the prey consumed by *A. brunneus* and *P. xaniurus* are pelagic. Demersal adult *P. xaniurus* eat mostly crustaceans (including pelagic pasiphaeid and sergestid shrimps), fishes (primarily myctophids), and cephalopods. Mesopelagic juveniles eat more and smaller pelagic pasiphaeid, euphausiid, and sergestid shrimps and cephalopods, and fewer fishes (Cailliet fn. 4). Similar pelagic prey also dominate the diets of *Galeus melastomus* and *Apristurus* spp., common outer shelf-upper slope scyliorhinid sharks of the northeastern Atlantic Ocean (Orsi and Wurtz 1977; Mattson 1981; Mauchline and Gordon 1983). Ontogenetic changes in diet were reported for *Scyliorhinus canicula*: the importance of crustaceans declines and the importance of teleosts increases with increasing fish size (Capapé 1974).

Deep-sea benthic fishes can obtain pelagic prey by 1) feeding on prey whose vertical distribution extends close to the bottom [*P. xaniurus* were observed eating moribund myctophids in the bottom of the Santa Barbara Basin (Springer 1979)]; 2) migrating into the water column to feed [*A. brunneus* and *P. xaniurus* are captured in midwater (Jones and Geen 1967; Lee 1969; UCSB fn. 3)]; 3) feeding on carcasses that sink to the bottom (mud and terrestrial plant debris were found in several catshark stomachs during the present study, and both species took dead bait); or 4) feeding in the net (not a factor in this study) (Pearcy and Ambler 1974; Pearcy 1976; Sedberry and Musick 1978).

ACKNOWLEDGMENTS

This study was supported in part by a contract from the County Sanitation Districts of Orange County. Special thanks are extended to the dory fishermen of Newport Beach for taking me on their boats. H. Stubbs, M. Moore, T. Pesitch, and the crews of the RV *Westwind* and RV *Vantuna* made the trawl collections possible. D. Tsukada and J. Laughlin diligently identified the prey organisms. G. Cailliet, P. Klimley, J. Seigel, and S. Springer provided helpful comments on earlier versions of the manuscript.

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FURTHER SUPPORT FOR THE HYPOTHESIS THAT INTERNAL WAVES CAN CAUSE SHOREWARD TRANSPORT OF LARVAL INVERTEBRATES AND FISH

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ABSTRACT

In areas of mesotides (tidal range 2 to 4 m) and narrow continental shelves (≤30 km) internal waves can transport (i.e., convey from one place to another) the larvae of coastal organisms shoreward. Research reported here was in an area of microtides (tidal range <2 m) and a wide continental shelf (>80 km), the South Atlantic Bight. Half of the sampled sets of internal waves were aligned parallel to shore and probably originated at the shelf break. The higher densities of larvae and flotsam in the slicks over these internal waves (convergence zones) than in the rippled water between slicks (divergence zones) indicates that these waves were transporting larvae and flotsam shoreward. All nontransporting internal waves were aligned at a sharp angle to shore and may have formed over shoals oriented perpendicular to shore.

To further test the hypothesis that internal waves can transport larvae, surface plankton were collected from the waters over, in front, and behind a set of internal waves. The density of *Portunus* spp. megalopae was significantly higher in waters in front of the set than behind. The average densities of a variety of larval fish and invertebrates were significantly higher over the internal waves than in front of the set of waves. These data indicate that internal waves can cause shoreward transport of larvae and flotsam. Precompetent larval fish were not carried shoreward by this set of waves while competent stages (i.e., juvenile through postflexion) were transported shoreward.

Recent papers have suggested that the planktonic larvae of some coastal invertebrates and fish (Shanks 1983, 1985, 1986; Jillett and Zeldis 1985; Kingsford and Choat 1986; Shanks and Wright 1987) as well as flotsam (e.g., an oil spill, Shanks 1987) can be transported (i.e., conveyed from one place to another) by internal waves. As the tide ebbs off the continental shelf or across some other sharp change in the bottom relief (i.e., a reef or bank) a lee wave is formed (Lee and Beardsley 1974; Gargett 1976; Maxworthy 1979). When the tide changes to flood this lee wave is "released" and propagates away from its point of origin (see for example Chereskin 1983). Most of the waves formed at the continental shelf break propagate shoreward. As the original internal wave moves onshore it evolves from a solitary wave into a set of waves (Osborne and Burch 1980). Stripes of glassy water, slicks, are surface manifestations of currents over the internal waves, and they delineate zones of converging and downwelling currents situated between the crest and the trough of an internal wave (Ewing 1950; LaFond 1959). The currents over the internal waves generate slicks by both perturbing small surface waves and concentrating the organic surface film (Ewing 1950; Gargett 1976). Buoyant flotsam will be carried into the convergence zone by the surface currents, but because of the particle's buoyancy they will not follow the water as it is downwelled; the flotsam will be trapped at the surface in the convergence and as the convergence zone moves onshore so will the flotsam. The proposed mechanism of larval transport suggests that any organism which can remain at the surface in the convergence zone either by swimming or other behaviors (Shanks 1985) will, like flotsam, remain in the slick and be transported onshore (Shanks 1983).

The conditions necessary for the production of tidally generated internal waves (tides, sharp bottom relief, and some water column density stratification) are present in the waters adjacent to nearly all land masses, and the surface manifestations of internal waves have been observed from both ships and satellites in numerous locations (Apel et al. 1975; Fu and Holt 1982; Sawyer 1983). Evidence that internal waves may be capable of transporting planktonic larvae onshore has been collected in the Pacific Ocean off Southern California (Shanks 1983, 1985, 1986), in the San Juan Archipelago (Shanks and Wright 1987), and in the waters off the North

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Manuscript accepted July 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

and South Islands of New Zealand (Zeldis and Jillett 1982; Jillett and Zeldis 1985; Kingsford and Choat 1986). These areas are characterized by mesotides, i.e., tidal range 2 to 4 m (Davis 1964). The first purpose of the research reported in this paper was to test if transport occurred in the Atlantic Ocean and in an area of microtides (tidal range <2 m, Davis 1964), the South Atlantic Bight.

To date researchers have compared the density (no./m^2) of larvae in the convergence zones (slicks) over internal waves to the density present in the divergence zone (ripples). Cases where the densities of larvae were significantly higher in slicks than the ripples were used as evidence for the proposed hypothesis. Higher density in the convergence implies that larvae tend to spend more time in the slick than in the water between slicks. Because of the speed at which internal waves are propagating, even a brief residence in an internal-wave-slick could cause appreciable shoreward transport. For example, if a larvae spent an hour in a slick it could be carried about 2 km (assuming an average internal wave speed of 56 cm/s, Sawyer 1983).

Higher larval densities in the convergence zone is only one of several predictions which should be true if internal waves are transporting larvae shoreward. The second purpose of this research was to test several additional predictions. As an internal wave moves shoreward, larvae from in front of the wave will be swept by the currents associated with the wave into the convergence zone. If these larvae can remain at the surface in the convergence, they will be carried shoreward. Predictions include 1) larval density in the waters in front of the set of internal waves should be significantly higher than in the waters behind the set; 2) because larvae will accumulate in the convergence, the observed density of larvae over an internal wave will be significantly higher than the density in the waters in front of the set of internal waves; and 3) a rare larval type may be carried into an area from a distant source in which case these particular larvae may only be present in the waters over the internal wave and will be concentrated in the slicks. To test these predictions, replicate neuston net samples were collected in the convergence and divergence zones over a set of internal waves, and in the waters immediately in front and behind this set of internal waves.

METHODS

The study was confined to the ocean waters at the northern end of Onslow Bay within about 20 km of Beaufort Inlet, NC, U.S.A. (long. 34°40′W, lat. 76°40′N; Fig. 1). Surface plankton tows from the waters over internal waves were collected during the summer of 1985 on 4 and 24 June, 14 and 20 July, and 21 August. On 24 June 1985 surface plankton tows were also collected from immediately in front and behind a set of internal waves. On 14 June 1985 and 9 and 19 June 1986 samples were collected at the surface and in the water column to determine which taxa were exclusively neustonic in distribution.

Winds stronger than 10 to 15 knots obliterate the slicks, which delineate the convergence zones over internal waves. Searches for internal-wave-slicks and sampling of the associated plankton were limited to periods with winds less than a moderate breeze (Beaufort scale 4). The procedure for locating internal-wave-slicks was to proceed along shore until the estuarine front associated with Beaufort Inlet was crossed and thence perpendicular to shore until we found a set consisting of at least three large (at least 30 m wide by about 500 m long) linear slicks separated by one to several hundred meters of rippled water. Sets of large slicks separated by rippled water are a unique surface signature of large, usually tidally generated internal waves (Ewing 1950; LaFond 1959; Apel et al. 1975; Gargett 1976; Fu and Holt 1982; Chereskin 1983; Sawyer 1983).

To test if a set of internal waves was capable of transporting flotsam, surface drifters (weighted Styrofoam cups) were released in a line perpendicular to and in front of the set of internal-wave-slicks (Shanks 1983). Prior to the release of the surface drifters and immediately after all sampling was completed the position of the first slick in the set was determined by either compass bearings on landmarks or with loran. From these measurements we were able to determine the distance that the set of waves propagated during the period of observation.

While the currents acted on these surface drifters, 3 or 4 replicate 5- to 10-min surface (<20 cm depth) plankton tows were made in the slicks and rippled water between slicks. These 1985 samples were collected on 4 and 24 June, 14 and 20 July, and 21 August 1985. In addition, on 24 June 1985 replicate surface plankton samples were also collected from the water immediately in front and behind the set of internal waves (within 200 m of the internal wave set). Plankton samples were collected using a manta net (Brown and Cheng 1981) with a mouth opening of 0.95 × 0.26 m and a net mesh of 0.333 mm. A flow meter mounted in the mouth of the net measured the volume of water filtered. Between tows

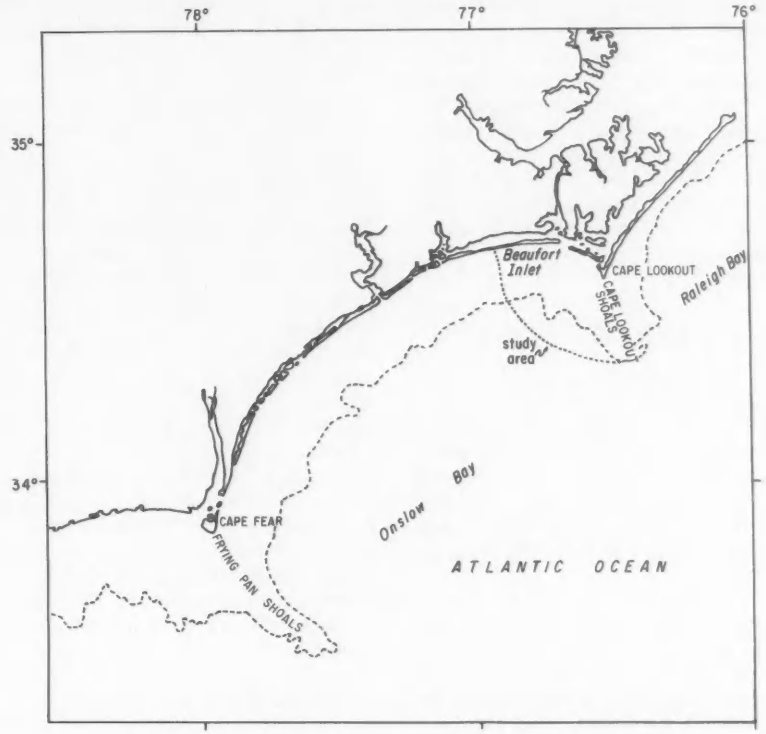

FIGURE 1.—Map of the study area. The dashed line running along shore is the 20 m contour and the dashed line running from just to the left of Beaufort Inlet to the tip of Cape Lookout Shoals encloses the study area.

in the different habitats the manta net was cleaned by towing for 5 to 10 minutes with the cod end removed. Most of the plankton was washed from the net by this procedure. For convenience and in order to more accurately sample the relatively small environments studied these plankton tows were made from a 6 m motor boat. Plankton samples were preserved in 5% formalin.

To assess the vertical distribution of larval types, surface and oblique plankton tows were made on 14 June 1985 and 9 June 1986. On 19 June 1986 replicate ($n = 3$) surface, oblique, and bottom tows were made. The dimensions of the oblique and bottom sled nets were 0.55 × 0.55 m and 0.80 × 0.45 m respectively. Both nets had mesh of 0.333 mm, and flow meters on the nets were used to measure the volume of water filtered. The procedure for the oblique tows was as follows: with the boat moving slowly forward the net was lowered rapidly to near the bottom (about 10 to 20 m) and then, maintaining a wire angle of about 60°, the net was hauled slowly to the surface. The bottom tows were made by lowering the sled straight to the bottom with the boat stationary; as the boat moved slowly forward, the line was paid out until a scope of 1 to 3 was achieved; tows lasted 5 to 10 minutes; at the end of the tow the boat was backed down onto the net; and the net was pulled vertically back to the surface. Both the oblique and bottom nets were open when they passed through the surface and were thus contaminated by some surface plankton.

Organisms were sorted and identified with the aid of a dissecting microscope. A variety of sources were used to identify larval fish (Fritzsche 1978; Hardy 1978; Johnson 1978; Martin and Drewry 1978; Fahay 1983). Larval fish were also sorted by developmental stage which were defined following the terminology and descriptions in Ahlstrom et al.

(1976) and Moser and Ahlstrom (1970). Megalopae were identified from references sited in Williams (1984). *Portunus* spp. and *Callinectes* spp. megalopae were separated using the characters suggested by Smyth (1980). Penaeids were identified using Cook (1966). No attempt was made to precisely identify the other groups of organisms counted.

Statistical comparisons of the density of larvae and flotsam in the different sampled habitats were made using Wilcoxon's two-sample test (Sokal and Rohlf 1969). Densities were considered to be significantly different when $P \leq 0.05$.

RESULTS

During the summer of 1985 searches for internal-wave-slicks were made on eight occasions. On three days, despite favorable wind and sea conditions, no internal-wave-slicks were observed. On 4 and 24 June, the observed sets of slicks were oriented parallel to shore and the bottom topography while on 14 and 20 July sets were oriented nearly perpendicular to shore. On 21 August a set of slicks aligned nearly perpendicular to shore was observed about 5 km offshore, and at about 9 km offshore a second set of slicks was found oriented parallel to the bottom topography. Both types of slicks, perpendicular and parallel orientation, possessed all of the usual characteristics of internal waves. Slicks were about 30 to 50 m wide, they were separated by one to several hundred meters of rippled water, and the sets moved (the parallel-to-shore slicks moved onshore while the perpendicular-to-shore slicks moved north).

The surface drifters released in front of sets of slicks oriented parallel to shore on 4 June and 21 August could not be located following the plankton tows. On 24 June, all of the drifters located at the end of the plankton tows (48 of 50 released) were found in the first two slicks of the set of internal waves. The drifters, which had been released in a 250 m long line in front of the set of internal waves, had been caught, concentrated, and carried about 4 km shoreward by the internal waves. Clearly this set of internal waves was capable of carrying buoyant flotsam shoreward.

Sargassum floats were abundant in the plankton tows. The floats are buoyant, do not extend above the water (i.e., are not blown directly by the wind), and, hence, the floats should act much like the released surface drifters. On all three dates when the internal-wave-slicks were oriented parallel to shore, the density of Sargassum floats was significantly higher (14- to 300-fold higher; Tables 1, 2) in the convergence than divergence zones. These data indicate that not only was the set of internal waves sampled on 24 June capable of carrying flotsam shoreward, but the sets oriented parallel to shore on 4 June and 21 August were also capable of carrying buoyant flotsam shoreward.

In contrast, on those days when the slicks were oriented roughly perpendicular to shore (14 July, 20 July, and 21 August, Table 1) released surface drifters were about equally distributed between slick and rippled water and, despite the fact that the slicks moved northward during the observation period, the drifters were not carried along with the waves. The density of Sargassum floats was not significantly higher in the slicks than the rippled water between the slicks. These data suggest that these internal waves were not transporting flotsam.

Before larval densities can be interpreted, it is first necessary to determine which larval types are found exclusively in the neuston. An increase in the neustonic density of organisms, which inhabit both the neuston and the water column, could be due to forces concentrating just the neustonic portion of the population, or it could be due to animals from the water column augmenting the population in the neuston. Given the sampling regime of this study it was impossible to differentiate between these two possibilities. Because of this limitation a series of tows were made in the neuston, the water column, and bottom water to determine which organisms exclusively inhabited the neuston.

There was a distinct assemblage of megalopae and larval fish that were caught in the oblique water column and bottom plankton tows but were nearly absent from the neuston tows (Table 3). Unfortunately, organisms that were common in the neuston tows made over or around internal waves were abundant on only one of the three dates when the vertical distribution samples were collected. On this one date (19 June 1986, Table 3) there was a group of larval fish and crabs that were only present in the neuston tows. This latter group included the megalopae of *Portunus* spp. and *Callinectes* spp., juvenile *Monacanthus hispidus*, and juvenile and larval *Hyporhamphus unifasciatus* and *Sphoeroides maculatus*. Previous research also suggests that these larvae and postlarvae as well as others are inhabitants of the surface waters. Both the behavior (Sulkin andVan Heukelem 1981) and the vertical distribution (Smyth 1980; Johnson 1985a) of *Callinectes* spp. megalopae suggest that they are usually neustonic. The megalopae of *Portunus* spp. and

TABLE 1—The density of larval fish and invertebrates (mean no./100 m^2 ± SE) in the slicks (convergence zones) and ripples (divergence zones) over internal waves and the relative concentration of these organisms in the slicks (i.e., the ratio of slicks/ripples) over internal waves oriented parallel (data in upper section of table) and perpendicular (data in lower section of table) to shore.

	Dates when slicks were oriented parallel to shore[1]					
	4 June 1985			21 August 1985		
	Slicks $n = 3$	Ripples $n = 3$	Slicks/ ripples[2]	Slicks $n = 3$	Ripples $n = 3$	Slicks/ ripples[2]
Total fish	12±2.9	4.2±0.9	3*	1.7±0.9	0.8±0.3	2
Hypsoblennius hentzi	6.0±2.1	3.1±0.2	2	0.1±0.1	0.4±0.1	0.3
Membras martinica	1.7±1.1	0.3±0.1	5	0	0	—
Hyporhamphus unifasciatus	0.7±0.7	0.6±0.4	1	0	0	—
Brevootia tyrannus	1.6–0.8	0	—	0	0	—
Monacanthus hispidus	0.9±0.6	0	—	0.8±0.6	0	—
Cheilopogen heterurus	0	0	—	0.2±0.1	0	—
Miscellaneous	1.1±0.3	0.3±0.2	4	0.4±0.4	0.2±0.1	2
Total Brachyura	41±12	1.7±0.6	24*	12±3.9	0.5±0.4	22*
Callinectes spp.						
Megalopa	0.2±0.2	0	—	3.9±1.7	0.2±0.1	19*
First crab	1.5±0.6	0	—*	0.2±0.2	0	—
Portunus spp.						
Megalopa	36±11	1.6±0.8	23*	7.5±21	0.3±0.3	24*
First crab	1.2±0.6	0	—	0	0	—
Miscellaneous	2.0±1.1	0.1±0.1	15*	0.3±0.2	0	—
Amphipods	40±16	1.2±0.1	33*	2.2±1.5	0	—
Polychaete larvae	5.2±1.7	0.7±0.5	8*	0	0	—
Stomatopod larvae	0	0	—	32±8.8	8.1±2.6	4*
Cnidaria	0	0	—	9.9±2.9	18±6.2	1
Salpa	0	0	—	15±2.6	60±2.9	0.3*
Sargassum floats	11±6.8	0.8±0.6	14*	8.8±1.4	0.4±0.3	21*

	Dates when slicks were oriented perpendicular to shore								
	14 July 1985			20 July 1985			21 August 1985		
	Slicks $n = 3$	Ripples $n = 3$	Slicks ripples[2]	Slicks/ $n = 4$	Ripples $n = 4$	Slicks/ ripples[2]	Slicks $n = 4$	Ripples $n = 4$	Slicks/ ripples[2]
Total fish	2.6±0.4	0.9±0.5	3*	1.2±0.3	1.0±0.2	1	1.1±0.1	1.8±1.0	1
Hypsoblennius hentzi	0	0	—	0.6±0.2	0.8±0.1	1	0.3±0.2	1.5±0.9	0.2
Hyporhamphus unifasciatus	0.5±0.3	0	—	0.4±0.2	0	—	0	0	—
Monacanthus hispidus	0	0.2±0.2	0	0	0	—	0.3±0.2	0.2±0.2	2
Cheilopogen heterurus	1.0±0.4	0	—	0	0	—	0.2±0.2	0	—
Miscellaneous	1.2±0.4	0.4±0.4	2	0.1±0.1	0.2±0.8	1	0.4±0.3	0.2±0.2	3
Total Brachyura	3.6±1.3	5.2±0.9	1	0.9±0.3	0.3±0.3	3	1.6±0.5	0.6±0.4	3
Callinectes spp.									
Megalopa	0.4±0.3	0.6±0.6	1	0.4±0.2	0	—	0.2±0.2	0	—
Portunus spp.									
Megalopa	0.9±0.6	2.2±0.6	0.4	0.2±0.2	0.2±0.2	3	0.1±0.1	0.3±0.3	0.5
Miscellaneous	1.8±0.7	2.2±0.1	1	0.1±0.1	0.2±0.2	1	1.4±0.5	0.3±0.2	5
Amphipods	5.7±3.9	2.9±0.6	2	4.4±0.7	1.7±0.8	3	0	0	—
Polychaete larvae	18±7.3	8.1±5.2	2	0	0	—	2.6±1.3	0.3±0.2	8
Stomatopod larvae	0	0	—	0	0	—	9.9–1.5	9.1±2.6	1
Cnidaria	83±15	126±73	1	0	0	—	7.8±1.2	4.9±1.7	2
Salpa	91±36	103±78	1	0	0	—	239±35	130±38	2
Sargassum floats	22±16	3.6±1.7	6	0.4±0.1	0.1±0.1	5	5.2±2.4	1.1±0.3	5

[1]Also included in this category are the data from 24 June (Tables 2 and 4).
[2]The ratio of the abundance in the slick divided by the abundance in the rippled water. * = $P \leq 0.5$ Wilcoxon's two-sample test (Sokal and Rohlf 1969).

Ocypoda spp. are abundant in neuston net tows (Smyth 1980; Johnson 1985a). Juvenile filefish, *Monacanthus hispidus*, are abundant in neuston tows (Fahay 1975; Eldridge et al. 1977) and are commonly found associated with floating seaweeds (Dooley 1972). Larval *Hyporhamphus unifasciatus* and *Hypsoblennius hentz* are abundant in surface plankton tows (Fahay 1975; Eldridge et al. 1977; Fritzsche 1978). Both their behavior (Breder and Clark 1947) and abundance in neuston tows (Eldridge et al. 1977) suggest that larval *Sphoeroides maculatus* are also residents of the surface waters. These results suggest that there is an assemblage of larvae unique to the neuston and that tests of the

internal-wave-mediated larval transport hypothesis outlined in the introduction can be made.

The distribution of organisms followed a pattern similar to that of Sargassum floats (Tables 1, 2, 4). In the tows from internal waves oriented perpendicular to shore there was only one instance in which the density of an organism was significantly higher in the convergence than the divergence zone (total larval fish, 14 July 1985, Table 1) indicating that these internal waves were not transporting larvae.

TABLE 2.—The density (mean no./100 m^2 ± SE) of invertebrates and Sargassum floats in front of the set of internal waves, the weighted average over the internal waves, in the internal wave slick (convergence zone), the rippled water between slicks (divergence zone), and behind the internal waves. Significance compares the density between these samples using a Wilcoxon's two-sample test.

	Density Mean no./100 m^2 ± SE, n = 3					Significance[1]		
Species	In front	Internal wave[2]	Slicks	Ripples	Behind	In front vs. behind	Slicks vs. ripples	In front vs. internal wave
Total Brachyura	1.1±0.2	6.5±1.3	21±5.7	2.5±0.2	0.2±0.2	*	*	*
Portunus spp.								
Megalopa	0.3±0	3.8±0.9	14±4.2	0.8±0.2	0	*	*	*
First crab	0	1.2±0.7	4.7±2.5	0.1±0.1	0		*	*
Callinectes spp.								
Megalopa	0.2±0.2	0.2±0.1	0.9±0.2	0	0.1±0.1		*	
Miscellaneous								
Megalopa	0.6±0.3	1.7±0.3	1.8±0.7	1.7±0.2	0.1±0.1			
Amphipods	30±8.1	176±112	754±546	0.3±0.3	20±6.5		*	
Polychaete larvae	2.9±1.1	16±3.0	62±8.6	2.5±1.3	1.8±0.6		*	*
Penaeus spp.								
Postlarvae	1.8±1.3	34±6.5	94±6.5	16±4.4	0.4±0.4		*	*
Sargassum floats	0.9±0.1	42±29	182±122	0.6±0.3	0	*	*	*

[1]Wilcoxon's two-sample test (Sokal and Rohlf 1969). * = $P \leq 0.05$.

[2]Weighted average density over an internal wave assuming a 30 m wide slick and a 100 m wide ripples. Internal wave = [(slick no./m^2 × 30 m^2) + (ripples no./m^2 × 100 m^2)/130 m^2] × 100.

TABLE 3.—Comparison of the density of various types of megalopae and larval fish caught in neuston, oblique, and bottom plankton tows.

	Density, no./100 m^2						
	14 June 1985		9 June 1986		19 June 1986 Mean ± SE, n = 3		
Species	Neuston	Oblique	Neuston	Oblique	Neuston	Oblique	Bottom
Crab megalopa							
Portunus spp.	0	0	0	0	5.3±4.5	0	0
Callinectes spp.	0	0	0	0	3.1±2.4	0	0
Ocypoda quadrata	0	9.0	0	0	1.5±1.4	0	0
Pinnotheridae	0.4	9.0	0	9.0	0.1±0.1	310±160	18.7±9.2
Xanthidae	0	88.8	0	9.0	0	690±250	17.0±9.6
Cancer spp.	0	0	0	0	0	66.7±40.6	1.4±0.8
Unknown and misc.	2.0	239	0.2	90.0	1.3±0.8	194±89.2	11.4±3.6
Fish larvae							
Monacanthus hispidus[1]	0	0	1.1	0	0.1±0.1	0	0
Hyporhamphus unifasciatus[1]	0	0	0	0	0.3±0.2	0	0
Sphoeroides maculatus	0	0	0	0	0.3±0.1	0	0
Membras martinica	0.4	0	0	0	0	0	0
Hypsoblennius hentzi	0	0	0	0	0.3±0.3	6.0±6.0	0
Symphurus plagiusa	0	44.4	0	27.0	0	190±60	0.1±0.1
Prionotus evolans	0	18.0	0	136	0	510±210	15.1±6.0
Seriola spp.	0	0	0	27.0	0	46.0±17.8	0.3±0.3
Engraulidae	0	18.0	0	217	0	280±99	16.2±8.9
Unknown and misc.	0	9.0	2.2	63.0	0	150±110	3.9±3.0

[1]Juvenile or late postflexion stages only.

TABLE 4.—The density (mean no./100 m^2 ± SE) of larval fish in front of the set of internal waves, the weighted average over the internal waves, in the internal wave slick (convergence zone), the rippled water between slicks (divergence zone), and behind the internal waves. Significance compares the density between these samples using a Wilcoxon's two-sample test. J = Juvenile, LPF = Late Post Flexion, EPF = Early Post Flexion, F = Flexion, PF = Preflexion, and Total = Sum of all stages.

	Density Mean no./100 m^2 ± SE, n = 3					Significance[1]		
Species	In front	Internal wave	Slicks	Ripples	Behind	In front vs. behind	Slicks vs. ripples	In front vs. internal wave
Monacanthus hispidus	1.1±0.1	2.0±0.4	8.1±9.0	0.2±0.2	0.1±0.1		*	*
Hyporhamphus unifasciatus								
J	0	0.1±0.1	0.2±0.9	0	0			
LPF	0.1±0.1	0.9±0.5	4.2±2.3	0	0			*
EPF	0	0.5±0.2	1.8±0.6	0	0		*	*
F	0	0.1±0.1	0.2±0.2	0	0		*	
PF	0	—	0	0	0			
Total	0.1±0.1	1.5±0.6	6.5±2.6	0	0		*	*
Membras martinica								
J	0	0.1±0.1	0.4±0.4	0	0			
LPF	0	—	0	0	0			
EPF	0	—	0	0	0			
F	0	0.1±0.1	0.5±0.3	0	0			
PF	0.2±0.1	0.2±0.1	14±4.2	0.4±0.4	1.0±0.6		*	*
Total	0.2±0.1	0.2±0.1	15±44	0.4±0.4	1.0±0.6		*	*
Hypsoblennius hentzi								
J	0	0.2±0.2	0.8±0.8	0	0			
LPF	0	0.2±0.1	0.5±0.3	0	0		*	
EPF	0	0.2±0.0	0.7±0.1	0	0		*	*
F	0.3±0.9	0.2±0.1	0.9±0.4	0	0		*	
PF	14±2.4	4.5±1.8	16±6.0	0.9±0.5	2.6±0.2	*	*	
Total	14±2.0	5.2±1.6	19±5.5	0.9±0.5	2.6±0.2	*	*	
Brevootia tyrannus								
F	0.2±0.1	0.1±0.1	0.5±0.3	0	0.2±0.2			
PF	0.7±0.2	0.2±0.1	0.6±0.3	0	0.1±0.1			
Total	0.9±0.3	0.2±0.0	1.1±0.1	0	0.4±0.4			
Miscellaneous								
J	0	0.5±0.2	1.8±0.9	0	0		*	*
LPF	0	0.2±0.1	0.8±0.9	0	0.1±0.1		*	*
EPF	0	—	0	0	0			
F	0.1±0.1	0.1±0.1	0.4±0.4	0	0			
PF	0	0.1±0.1	0.4±0.4	0	0			
Total	0.1±0.1	0.8±0.2	3.4±1.0	0	0.1±0.1		*	*
Grand total	16±1.6	13±1.0	53±3.6	1.6±0.2	4.2±0.4	*	*	

[1]Wilcoxon's two-sample test (Sokal and Rohlf 1969). * = $P \leq 0.05$.

[2]Weighted average density over an internal wave assuming a 30 m wide slick and a 100 m wide ripples. Internal wave = [(slick no./m^2 × 30 m^2) + (ripples no./m^2 × 100 m^2)/130 m^2] × 100.

In contrast, in tows from internal waves oriented parallel to shore there were numerous instances in which larval densities were significantly higher in the slicks (Tables 1, 2, 4); the densities observed in the slicks were 4- to >50-fold higher than those in the rippled waters. These data demonstrate that a variety of larval and postlarval invertebrates and fish were transported shoreward by these internal waves.

On 24 June 1985, surface plankton samples were collected in the first two slicks over a set of internal waves oriented parallel to the shore, in the rippled water between these slicks, and in front and behind the entire set of internal waves. Ninety-six percent of the surface drifters were caught by the first two convergence zones and carried shoreward about 4 km. The density of Sargassum floats was highest in the slicks (>100-fold, Table 2) and they were at significantly lower densities behind the set of internal waves than in front. There were 0.9 Sargassum floats/100 m^2 in the waters in front of the set of internal waves and none in the waters

behind the waves (Table 2). The distribution of tar balls (spilled asphalt) over and around the internal waves was similar to the distribution of Sargassum floats (Shanks 1987). As these internal waves propagated shoreward, the currents over the waves swept buoyant flotsam from the waters in front of the set of waves into the convergence zone where the flotsam was caught and carried shoreward.

Calculation of the density of larvae or flotsam over the internal waves (i.e., density in the slicks plus the ripples) requires knowledge of the width of the slick and rippled waters over the internal waves. Unfortunately, in this initial study these measurements were not made, necessitating that these widths be approximated using values from the literature. Slicks were assumed to be 30 m wide and the rippled waters separating the slicks were assumed to be 100 m wide. These values are consistent with my experience and with published values (LaFond 1959; Sawyer 1983). The observed density over one internal wave was calculated as (slick no./m^2 × 30 m) + (ripples no./m^2 × 100 m)/130 m^2. The density over an internal wave was compared with the density in an equal area of water in front of the set of internal waves. Making these calculations for Sargassum floats gives an observed density of 42 floats/100 m^2 over the internal wave vs. 0.9 floats/100 m^2 in front of the set; the density over the internal wave is significantly larger (46-fold greater) than the density in front of the set (Table 2). Again the data indicate that Sargassum floats were carried shoreward by the internal waves.

None of the types of larval fish characteristic of water column samples (Table 3) were caught in any neuston tow. Present in the neuston tows were only those types of larval and juvenile fish which my samples and the descriptions in the literature suggest are characteristically neustonic.

The densities of larval and juvenile fish frequently were significantly higher in the slick samples than the samples from the rippled waters between slicks (Table 4). On 24 June 1985, most larval fish, especially juvenile and postflexion stage larvae, were rare in both the waters in front and behind the set of internal waves. On this date in 6 tows, 3 in front and 3 behind the set of internal waves, only 4 juvenile and postflexion larvae were caught as compared to 185 in the 3 tows made in the slicks. Probably because of the rarity of larval fish in both in front and behind tows there were only three cases, total and preflexion *Hypsoblennius hentz* and total larval fish, in which the density of fish in front of the set of internal waves was significantly higher than behind the set (Table 4). There are seven instances, however, in which the density over the internal wave of a larval or juvenile fish was significantly and at least 10-fold higher than the density in front of the set of internal waves (Table 4). In six of these instances the fishes were at the juvenile, late postflexion, or early postflexion stages of development.

Larval and juvenile fish were grouped by stage of development and the densities over and in front of the internal waves were calculated for each developmental stage (Fig. 2). The densities over the internal waves of the juvenile, late postflexion, and early postflexion developmental stages were significantly higher than the densities of these stages in front of the set. There was not a significant difference between the densities over and in front of the set of internal waves of flexion stage larvae and preflexion larvae were significantly more abundant in front of the set. These data suggest that internal

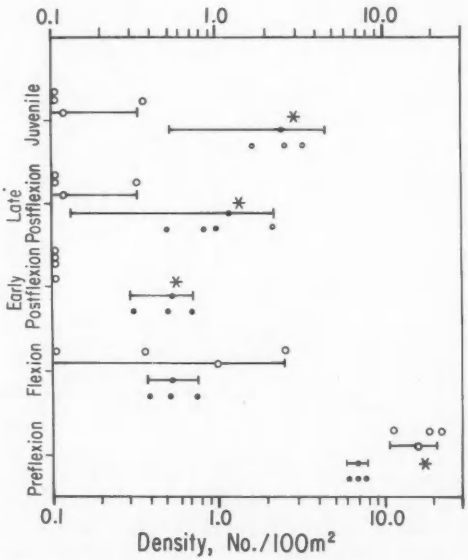

FIGURE 2.—Densities of larval fish by stage of development caught on 24 June 1985 in the waters in front of the set of internal waves (open circles) and over the internal waves (closed circles). Data are presented as the mean ±95% confidence interval with the points above or below this line being the actual observations. Asterisks indicate cases where the in front density was significantly different (Wilcoxon's two-sample test, $P \leq 0.05$) from the density over the internal waves. The method of calculating the densities is described in the text.

waves are capable of carrying fish larvae shoreward, but shoreward transport seems to be confined to postflexion stage larval or juvenile fish.

In the samples from 24 June 1985 there are a number of cases in which a fish species and/or stage of development was common in the tows from the convergence zones but was absent or very rare in the divergence zones, in front, or behind the set of waves (i.e., zero or one caught in the nine tows from these three habitats, Table 4). Either these larval fish are extremely rare in the waters surrounding the internal waves in which case the convergence zone must have accumulated larvae from a large volume of water or the internal waves transported the larvae into the study area from a distant source.

On 24 June 1985, the density of total Brachyura was significantly higher in the slicks over the internal waves than in any other area sampled (Table 2). *Portunus* spp., a group which previous data had demonstrated inhabited the neuston, made up the bulk of the Brachyura caught. The densities of *Portunus* were significantly higher in the slicks than the rippled water between slicks. The density of *Portunus* spp. megalopae differed significantly from 0.3/100 m^2 in front of the set of internal waves to 0/100 m^2 behind (Table 2). *Portunus* spp. first crabs were absent from both the waters in front and behind the set of internal waves; they were abundant in the waters over the internal wave (Table 2). The densities over the internal waves of *Portunus* spp. megalopae and first crabs were significantly higher than their densities in front of the set of waves (Table 2). *Callinectes* spp. were uncommon in the samples though their density was significantly higher in the slick than in the rippled waters. Included under the category of miscellaneous megalopae were the species *Uca* spp., *Sesarma* spp., and majid crabs, all forms which were found to be more abundant in the water column than in the neuston (Table 2). There was not a significant difference between their density in the slicks vs. the rippled waters, suggesting that these megalopae were not carried shoreward by the sampled set of internal waves. The data indicate that definitely *Portunus* spp. and possibly *Callinectes* spp. were carried onshore by the sampled set of internal waves.

Other organisms counted in the samples were adult amphipods, polychaete larvae, and *Penaeus* spp. postlarvae. Densities of these types of organisms were significantly higher in the slicks than the rippled waters (Table 2). While in each instance densities were lower behind the set of internal waves than in front, the differences were not statistically significant. The density of polychaete larvae and *Penaeus* spp. postlarvae over the internal waves were significantly higher than the density in front of the set. These data suggest that these invertebrate larvae were also transported onshore by the set of internal waves.

DISCUSSION

Tidally generated internal waves have been observed in many areas of the world (Apel et al. 1975; Fu and Holt 1982; Sawyer 1983). Larvae may utilize internal waves as a mechanism of onshore migration along many coastlines. Testing this hypothesis would require the impossible task of making observations along all coastlines. An alternate technique is to test for internal wave transport in areas with different combinations of tidal range and shelf width. Previous work has been done in areas of mesotides (tidal range 2 to 4 m, Davis 1964) and either narrow (<6 km, Shanks 1983) or moderate (about 30 km, Kingsford and Choat 1986) shelf widths. The Atlantic adjacent to the Beaufort Inlet is characterized by microtides (tidal range <2 m, Davis 1964) and a wide shelf (about 80 km). The first purpose of this research was to test if onshore transport of larvae could occur in an area with these characteristics. On the three dates in which the internal-wave-slicks were oriented roughly parallel to shore the data suggest that internal waves were transporting larvae and flotsam onshore. If the waters around the Beaufort Inlet are representative of localities with microtides and wide shelves, then onshore migration of larvae via internal waves may occur in other similar areas of the world.

On three dates the internal-wave-slicks were oriented nearly perpendicular to shore and were propagating roughly northward. Over the continental shelf, internal waves oriented roughly perpendicular to shore have been observed in satellite photographs. These internal waves are invariably associated with submarine canyons (Apel et al. 1976). There are no submarine canyons in Onslow Bay. The internal waves causing these slicks may have been formed over Frying Pan Shoals (Fig. 1). These shoals extend about 50 km across the shelf from the end of Cape Fear and form the southern boundary of Onslow Bay. Just north of the study area, Cape Lookout and the Cape Lookout Shoals also extend out across the shelf (Fig. 1). On a flight over Cape Lookout numerous slicks oriented parallel to Cape Lookout Shoals were observed propagating northward into Rayleigh Bay (pers. obs.). The geography

and oceanography of the Cape Lookout and Frying Pan Shoals are so similar that by analogy the internal waves oriented perpendicular to shore observed during this study may have been formed over Frying Pan Shoals and propagated northward into Onslow Bay. The mechanism for the formation of these internal waves is unknown.

As was observed in a previous study (Shanks 1983), only some sets of internal waves transported larvae or flotsam. In this study only those slicks aligned parallel to shore caused transport. It is not clear why some sets of waves cause transport while others do not. The physical characteristics of tidally generated internal waves are quite variable. The amplitude (Cairns 1968) and decay distance of internal waves varies over the fortnightly tidal cycle (Brink 1988). Further, the depth, wave length, and shape of the internal waves is dependent on the relative depths of the thermocline and the bottom and wave amplitude (LaFond 1959; Lee 1961; Cairns 1967, 1968). What is needed is simultaneous measurements of the physical characteristics of a set of internal waves much like those made by LaFond (1959) with measurements of the transport of flotsam or larvae.

The second purpose of this research was to test several new predictions derived from the hypothesis that internal waves can transport larvae. If transport was occurring, then one would predict that 1) due to the accumulation of larvae in the convergence zones as internal waves propagate shoreward, the density of larval types transported by the internal waves should be significantly lower behind than in front of the set, 2) the observed density of larvae over an internal wave should be significantly higher than in the waters in front of the set of waves, and 3) there may be types of larvae which are only present in the slicks, suggesting that they had been carried into the area from a distant source. The appropriate samples to test these three predictions were collected on 24 June 1985. The densities of several larval types were significantly higher in the waters in front of the internal wave set than behind. There were many instances in which the observed density over the internal waves of a type of larvae was significantly higher than in the waters in front of the set of internal waves. Lastly, there were a number of organisms that were only caught in the convergence zones over the internal waves. In this set of observations the three predictions were confirmed indicating that this set of internal waves was carrying larvae and flotsam shoreward.

The significant differences in larval densities observed on 24 June (i.e., in front vs. behind and over the internal waves vs. in the front of the set of waves) may have been due to fortuitous cross-shelf patchiness in larval density. Because conditions allowed only one opportunity to sample in front and behind a set of internal waves, this alternate explanation can not be rejected. Cross-shelf larval patchiness is, however, probably not an adequate explanation because of the very short distance over which large differences in larval abundances were observed. For example, the tows in front of the set and the tows in the slick and rippled water over the set were separated by at most 200 m, yet there were many cases (14, Tables 2, 4) where larval abundances were different by at least a factor of 10. Differences in plankton abundance of this magnitude and over this small a distance are almost always associated with oceanographic features (e.g., fronts: Boden 1952; Pingree et al. 1974; Owen 1981; Fogg et al. 1985). The only apparent oceanographic feature in the study area was the internal-wave-slicks. The observed differences in larval density were probably caused by the internal waves.

The data in Figure 2, the density of fish by stage of development over the internal waves vs. in front of the set of waves, suggest that only the later developmental stages of fish (juvenile through early postflexion) were transported onshore by the set of internal waves sampled on 24 June 1985. All five of the abundant fish species (Table 4) inhabit near shore or estuarine habitats as adults (Fritzsche 1978; Hardy 1978; Johnson 1978; Martin and Drewry 1978). Flexion and preflexion larval fish are clearly not competent to adopt the adult or nursery habitat, and the data suggest that they were not carried onshore by the internal waves. There may be adaptive advantages to planktonic larvae avoiding estuarine waters during their development (Strathmann 1982). Juvenile fish and, perhaps, also postflexion larvae, are competent to recruit into the adult or nursery habitat. Transport onshore by internal waves may, therefore, be adaptively advantageous for those fish whose adult or nursery habitat is coastal or estuarine.

The larval development of the blue crab, *Callinectes sapidus*, occurs at sea (Smyth 1980; McConaugha et al. 1983; Johnson 1985b). The larvae are present in the waters over the continental shelf and out to the Gulf Stream (Smyth 1980). At the end of the larval period the megalopae must return to an estuarine habitat to continue its adult existence. How the megalopae make this migration is an open question (Johnson et al. 1984; Johnson

1985b). The behavior of the megalopae (Sulkin and Van Heukelem 1981) and their distribution in the plankton (Smyth 1980; Johnson 1985a) both suggest that these larvae are inhabitants of the neuston. Larvae that inhabit the neuston can be transported onshore by internal waves (Shanks 1985). On 4 and 24 June and 21 August the densities of *Callinectes* spp. megalopae and first crabs were significantly higher in the convergence zones over the internal waves than in the divergences, suggesting that *Callinectes* spp. were being transported onshore by the sampled internal waves. On 24 June, when *Callinectes* spp. were uncommon, there was not a significant difference in the density of *Callinectes* spp. in front vs. behind the internal wave nor was there a significant difference in the density of blue crabs over vs. in front of the set of waves. These results are mixed, but they do suggest that the megalopae of *Callinectes* spp. may be transported shoreward in the convergence zones over internal waves.

The megalopae of a variety of crab species were only caught in the water column (Table 3 and see Johnson 1985a). Some of these megalopae as adults occupy near shore and even estuarine habitats. If these megalopae migrate onshore they must be utilizing some mechanism of onshore transport other than slicks over internal waves.

In conclusion, the data presented in this paper indicate that in an area where the tides are of small amplitude and the continental shelf is wide, internal waves are nevertheless capable of transporting larval invertebrates and fish shoreward. The samples collected on 24 June 1985 more critically test the hypothesis that internal waves cause cross-shelf transport and the results support the hypothesis.

ACKNOWLEDGMENTS

Assistance with the field work was enthusiastically provided by O. McMillan, G. Safrit, J. Purifoy, and W. Graham. G. Safrit, in addition, heroically and with really very little complaint, sorted most of the plankton samples. Comments by M. Kingsford and R. Forward improved the manuscript. Figures were prepared by V. and H. Page and F. Schwartz helped to identify larval fish.

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TROPHIC RELATIONS OF THE BLUE ROCKFISH, *SEBASTES MYSTINUS*, IN A COASTAL UPWELLING SYSTEM OFF NORTHERN CALIFORNIA

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ABSTRACT

The planktivorous *Sebastes mystinus* in nearshore habitats off northern California feeds primarily on relatively large, gelatinous zooplankters that originate offshore, including thaliaceans, ctenophores, and pelagic hydrozoans. These prey organisms increase in number during spring and summer when surface waters driven seaward by northerly winds carry upwelled nutrients to diatoms that nourish offshore zooplankton populations. But the resulting increases in zooplankton during this upwelling season become available to *S. mystinus* in the nearshore habitats only when the surface flow turns shoreward during intermittent episodes of downwelling. Although some of this shoreward flow is driven by southerly winds, much of it occurs during calms, or under northerlies lacking the velocities needed to drive surface waters seaward. There is increasing shoreward transport during fall and winter, when downwelling episodes are more frequent, but progressively fewer zooplankters are carried into the nearshore habitats. This is because as less nutrients come into the system with the reduced upwelling, and as available sunlight declines, the offshore zooplankton populations suffer from shortages of diatoms. Although *S. mystinus* compensates for decreased numbers of zooplankters during most of the year with increased consumption of specific plant materials, i.e., *Nereocystis sori*, or the monostromatic epiphytes *Porphyra nereocystis* and *Smithora naidum* (depending on the season), these too are in short supply during winter. In winter, therefore, *S. mystinus* experiences its poorest feeding conditions. Thus, *S. mystinus* is adapted to feeding opportunities created by alternating episodes of strong upwelling and strong downwelling, and is most abundant within its range along the west coast of North America where both conditions are well developed.

Coastal marine fishes in temperate latitudes experience major seasonal changes in their environment. In study off northern California's Mendocino coast (lat. 39°13′N, long, 123°14′W), we studied the effects of seasonal change on the trophic relations of the blue rockfish, *Sebastes mystinus* (Fig. 1). *Sebastes mystinus*, a major species in the recreational fishery off northern and central California (Frey 1971), is a planktivore that feeds on scyphozoans, ctenophores, copepods, amphipods, thaliaceans, fishes, and algae (Gotshall et al. 1965; Love and Ebeling 1978; Hallacher and Roberts 1985). Although its diet is known to vary with the season, relationships involving specific environmental features, and the availability of prey, remain unclear.

The marine environment off California is profoundly affected by seasonal variations in wind-driven movement of the surface water (Reid et al. 1958; Bolin and Abbott 1962; Bakun and Parrish 1980). This force, known as Ekman transport (Ekman 1905), is strongest off the Mendocino coast (Bakun 1973), where it must be a major influence on the trophic relations of *S. mystinus*. Because Ekman transport is the basis of coastal upwelling (e.g., Smith 1968), it is of great importance to biological productivity (e.g., Boje and Tomczak 1978) and, therefore, to the availability of food.

Upwelling develops along the coast of northern California when surface waters driven seaward by northerly winds, such as those characteristic of spring and summer, are replaced by colder subsurface waters from offshore that flow up into the nearshore habitat (Smith 1968; Bakun 1973). On the other hand, an opposing condition develops when surface waters driven shoreward by southerly winds, such as those characteristic of winter storms, flow over the colder nearshore waters to produce the condition sometimes called downwelling (Bakun 1973). But despite the strong seasonality evident in both upwelling and downwelling, short-term reversals lasting just a few days occur throughout the year (see Bakun [1973] and Mason and Bakun [1986]).

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Manuscript accepted July 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

FIGURE 1.—*Sebastes mystinus* next to canopy of bull kelp, *Nereocystis leutkeana*, off Mendocino.

In this paper we consider how the trophic relations of *S. mystinus* respond as seaward and shoreward movements of the surface water produce alternating episodes of upwelling and downwelling. Emphasis is on how the resulting environmental changes alter the relative availability of food. Among studies of marine fishes, this is, to our knowledge, the most comprehensive attempt yet made to integrate data on food, potential food, and environmental variables—all key elements in trophic relations.

METHODS

The study lasted from the winter of 1976–77 to the summer of 1981, with the first 15 months involving exploratory work along about 15 km of the Mendocino coast south of Point Cabrillo. A study site was then established off Salmon Point (Fig. 2) during the spring of 1978, and from that time sampling followed a set regime.

Study Site

The study site (Fig. 3) was in 10–15 m of water, about 300 m from shore. Rocks the size of houses jutted 10–15 m above the water at the seaward perimeter of the site, but despite the shelter offered by these rocks, most of the area was regularly swept by wind and sea. Except for isolated pockets of sand, the site was floored by rock pavement and boulders (some 5–15 m in diameter), largely swept clean by the turbulence and surge that prevailed most of the time.

Environmental Variables

During each sampling session, we noted the gen-

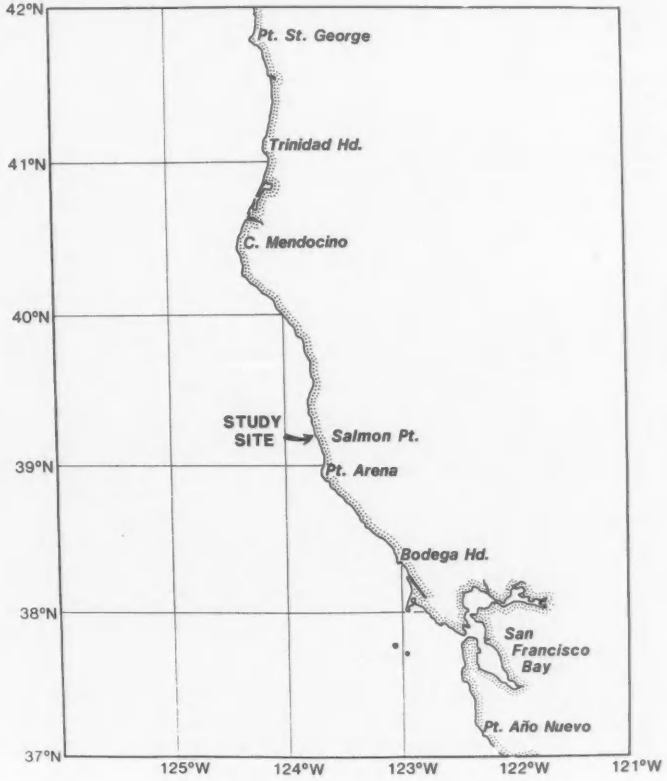

FIGURE 2.—The coast of northern California.

eral state of the weather, including wind direction and estimated velocity. In this paper (except in Figures 4 and 9, as noted below) we consider winds from between northwest and northeast to be "northerly", and from between SW and SE to be "southerly". We also noted sea conditions and recorded sea-surface temperatures. More precise wind data became available after May 1980, when a NOAA weather station was established at Mendocino. During the same month, we placed recording thermographs at depths of 6 and 20 m in the study area, and although the deeper site was abandoned after 1981 in favor of replicating the record with two instruments at the shallower site, these have given us a continuous record of water temperatures from then until the present (Spring of 1988). Based on these observations and in situ visual assessments of the plankton and water characteristics, usually we could tell whether upwelling or downwelling predominated during a sampling session even though most of the time conditions were to some extent mixed.

Diet and Occurrences of Food

To relate the diet of *S. mystinus* to foods present at the time of feeding, we took concurrent samples of gut contents and plankton, as well as some selective samples of the benthos. Complications from normal diel variability were reduced by taking all samples between the hours of 1100 and 1300. The sampling schedule was strongly influenced by the weather, as much of the time work was prevented by high seas and/or long-period swells and result-

FIGURE 3.—Study site off Salmon Point.

ing turbulence. Although all seasons were sampled, most collections and observations were made when the sea was relatively calm, a condition that generally lasted no more than a few days at a time. Nevertheless, because often the weather turned while observations were under way, turbulent conditions were well represented.

Fish

The *S. mystinus* studied at Mendocino were spatially segregated by size and age. This paper considers only adult fish of more than 200 mm SL, which forage by day in aggregations of up to several hundred individuals in the upper levels of the water column. The analysis of gut-contents involved 247 individuals, 200–350 mm SL, taken from these aggregations using handheld spears. Juveniles and subadults are excluded because they forage at lower levels of the water column and consume organisms not taken by adults.

Plankton

Most sampling sessions included two plankton collections: one at the sea surface, and the other between 1 and 2 m above the sea floor. Only the 27 surface collections are considered here, however, because the others sampled at levels of the water column below where adults usually feed. For each collection we used scuba to push the net (0.333 mm mesh in a 78 cm × 78 cm frame) through the water for 5 minutes. Occasionally the net broke the surface, but usually was kept underwater to avoid fouling the sample with floating debris. (See Hobson and Chess 1976 for additional information on this pro-

cedure, and how the samples were processed and analyzed.) We visually assessed the larger zooplankters in the water column during each collection, as well as at other times during each sampling session, and these observations greatly enhanced our ability to interpret the samples.

Benthos

Although *S. mystinus* is a planktivore, it is important to include the benthos when documenting environmental changes that affect its feeding. Many of the actual or potential foods of *S. mystinus* originate on the underlying substrata, and their occurrences in the water column relate to changes in the benthos. Thus, assessments of the benthos done during other studies concurrently under way in the study area, including visual counts and airlift samples, produced data that are incorporated into this report where pertinent.

Ranking Prey Taxa

To estimate the relative importance of the various prey organisms in the diet of *S. mystinus*, we grouped related forms in multispecies categories that were then ranked. The ranking was based on an index calculated as: relative frequency of occurrence in diet × mean number of individuals consumed × percent of total diet volume that was represented by that category. This index is similar to the widely used Index of Relative Importance (IRI) of Pinkas et al. (1971), but puts more weight on numbers consumed. It is important to emphasize numbers consumed in quantifying the feeding activity of *S. mystinus* (and most other planktivores) because the many small prey are ingested individually, making the capture of each a discrete act.

RESULTS

During the four years of this study, spring and (to a lesser extent) summer constituted an upwelling season, while fall and (to a greater extent) winter constituted a downwelling season. The spring transition between downwelling and upwelling seasons occurred over just a few days between late March and early April, whereas the less distinct fall transition between upwelling and downwelling seasons was extended over a month or more between mid-August and late October.

Despite this seasonal pattern, however, there were short-term reversals of just a few days that had profound effects. Reactions of the environment to major wind changes were virtually immediate. Sharply reduced water temperatures signifying the intrusion of upwelled water often followed within hours of increased northerly winds, while warmer water rich in such readily visible zooplankters as ctenophores, hydrozoans, pteropods, thaliaceans, and larvaceans, often flowed into the nearshore habitats within a day after the onset of southerly winds. Conditions during each sampling session are listed in Table 1.

Although downwelling conditions were most intense under southerly winds, they also developed during calms and with weak northerlies. We found that generally it took northerlies of 10 knots (K) or more to produce upwelling conditions, although as little as 5 K were effective if held steady for several days. In the absence of sufficient force, however, upwelling ceased and warmer water rich in offshore zooplankters entered the nearshore habitat, generally moving in a southerly direction along the coast.

The close relation between shifts in prevailing wind and alternations between upwelling and downwelling is illustrated by comparing the wind direction and velocity measured by the nearby NOAA weather station to the sea temperatures recorded by our thermographs. Although these data became available only during the last year of the study, subsequent years have produced similar profiles (except 1982–83, when there was a strong El Niño). Thus, the pattern of sea temperatures and wind during the upwelling season of 1981 and during the downwelling season of 1980–81, recounted in detail below, are representative.

The Upwelling Season

The upwelling season began in late March or early April with a precipitous drop in sea temperatures. It was a drop of about 3°C—typically from 11°–12°C to 8°–9°C—that coincided with the onset of strong, persistent northerly winds characteristic of this time of year. The pattern of sea temperatures and wind during the 1981 upwelling season (Fig. 4) illustrates how upwelling and downwelling related to prevailing winds during that period.

Habitat Conditions

At the start of the upwelling season, the nearshore habitats appeared barren. Storm seas during the previous winter had carried away most of the bull

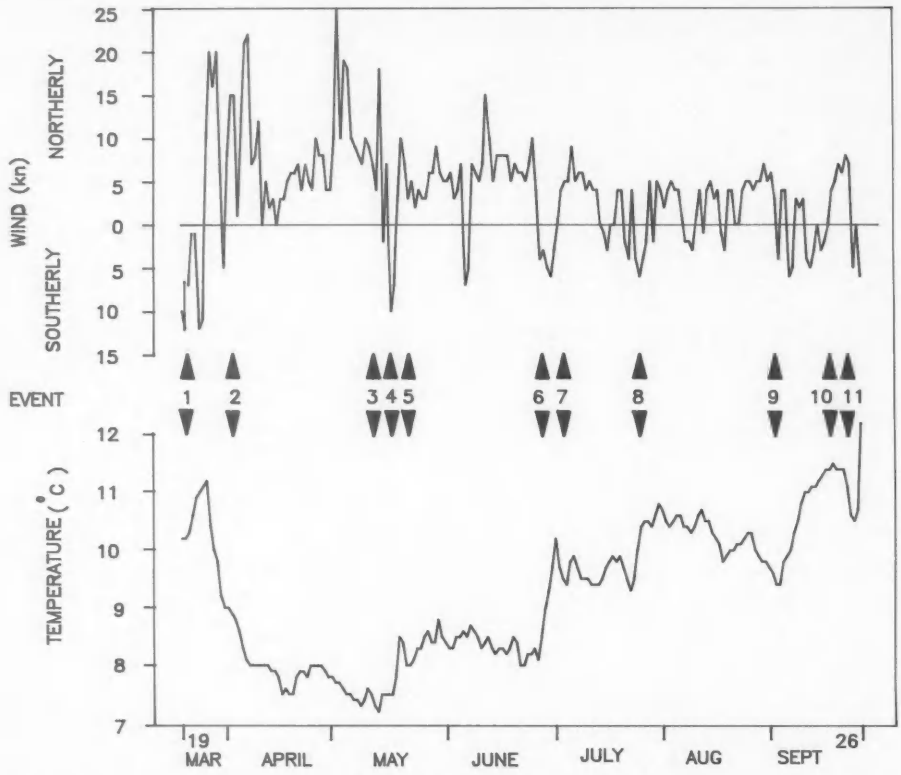

FIGURE 4.—Sea temperatures and wind off Mendocino during the 1981 upwelling season. *Plotted sea temperatures* are estimated daily means from record of continuously recording thermograph. Plotted wind velocities and directions are averages of 2–5 daily readings. Southerly values represent winds from south of east-west axis, northerly values represent winds from north of this axis. The highly infrequent winds from due west or due east were entered as zero. In calculating values for days of both northerlies and southerlies, the former were considered positive, the latter negative. The following accounts of events identified in the figure cite wind velocities that exceed plotted values, which are averages.

EVENT 1—Seven days of southerly winds, 19–25 March, with sea temperatures rising to 11.1°C, represented the last downwelling episode of the 1980–81 downwelling season.

EVENT 2—The 1981 upwelling season began on 26 March, as 2 weeks of strong northerlies (to 4 April) resulted in an abrupt drop of more than 3°C in sea temperature.

EVENT 3—Water temperatures fell to the lowest point of the year, 7.3°C, on 13 May following over 2 weeks of 10–30 K northerlies.

EVENT 4—The first of a series of downwelling episodes during this upwelling season developed as 8–12 K southerlies on 17 and 18 May resulted in a sharp rise in sea temperature to 8.5°C.

EVENT 5—Temperatures dipped when the wind shifted back to the north on 19 May. Over the next month variable northerlies blew at less than 10 K, and although sea temperatures did not vary more than a few tenths of a degree, they were consistently about 1°C warmer than before the 17–18 May downwelling episode.

EVENT 6—On 28 June, the first of 6 consecutive days of 4–10 K southerlies, sea temperatures began a steep climb to above 10°C that marked the upwelling season's second major downwelling episode.

EVENT 7—Northerlies returned on 3 July, and sea temperatures immediately dropped below 10°C again. Despite northerlies of 5–7 K over the next 2 weeks, sea temperatures remained at about 9.5°C, again about 1°C warmer than before the 28 June–2 July downwelling episode.

EVENT 8—With southerlies of 5–10 K on 7 of the 9 days between 12 and 20 July, sea temperatures once again rose above 10°C to mark the season's third major downwelling episode.

TABLE 1.—Conditions during sampling sessions off Salmon Point, Mendocino County, 1978–81.

Date	Sea temp. (°C)	Wind dir. : vel. (knots)	Plankton condition[1]	Fish sampled		
				No.	Size range (mm)	Mean (mm)
I. Upwelling season, upwelling conditions						
5/10/78	8.5	NW: 10	U/M	7	270–312	289.7
8/08/78	10.5	NW: 10	U	6	285–309	293.0
6/12/79	9.0	NW: 15	U/M	7	241–312	239.3
6/24/80	10.0	None	U	9	224–308	250.0
4/09/81	8.1	NW: 15	U	8	235–300	265.6
5/19/81	9.5	WNW: 10	U/M	1	260	260.0
6/17/81	9.0	NNW: 10	U	13	260–336	301.0
II. Upwelling season, downwelling conditions						
6/21/78	9.0	None	D/M	3	228–308	270.3
6/29/78	10.0	SW: 2	D/M	6	240–315	254.7
8/23/78	11.0	None	D	6	230–280	259.0
9/08/78	14.0	None	D	4	240–295	277.5
4/24/79	10.0	None	M	9	225–313	277.7
7/24/79	11.5	None	M	11	208–302	239.5
8/27/79	12.8	NW: 5	M	12	204–335	264.6
5/29/80	9.5	None	D/M	20	213–330	276.4
7/17/80	11.0	NW: 5	D/M	5	240–304	270.8
8/21/80	11.0	S: 5	D	9	230–305	270.6
III. Downwelling season, downwelling conditions, fall						
10/04/78	11.0	WNW: 10	D+	3	270–310	286.7
10/18/78	12.0	S: 5	D+	9	220–350	296.2
12/08/78	9.0	S: 8	D+	17	227–331	281.2
10/16/79	14.0	NW: 8	D	13	218–311	280.1
11/04/80	12.0	N: 6	D	17	230–335	296.6
12/17/80	12.0	NNW: 5	D	14	225–331	276.3
IV. Downwelling season, downwelling conditions, winter						
2/04/79	10	S: 12	D	12	231–320	273.3
3/06/79	11	W: 8	D	2	224–260	242.0
1/31/80	11	None	M	16	200–345	275.3
1/13/81	13	SW: 5	D	8	275–305	286.3

[1]Plankton condition. D = Downwelling condition: zooplankters considered to be offshore species, especially relatively large gelatinous forms, numerous. U = Upwelling condition: offshore zooplankters absent. M = Mixed condition: some offshore zooplankters present.

kelp, *Nereocystis leutkeana*, which is the major component of the kelp forests. These same seas, often heavily laden with sediment, had also scoured the seafloor of much of the algal understory, as well as many of the sedentary invertebrates. Once the upwelling season had been established, however, the habitats changed rapidly.

Often during early-season upwelling the water was relatively transparent, although after rains visibility often was limited by suspended sediment discharged into the nearshore habitat from coastal streams. By mid-May, however, the numbers of planktonic diatoms (primarily *Chaetoceros* sp. and *Nitzchia* sp.) had greatly increased to depths of

EVENT 9—In the last major upwelling of this upwelling season, sea temperatures fell to 9.4°C on 2 September after 10 consecutive days of 5–8 K northerlies.

EVENT 10—Sea temperatures rose steadily to 11.4°C on 17 September after 1–3 day periods of 4–8 K northerlies had alternated with 1–4 day periods of 4–8 K southerlies through the first half of that month.

EVENT 11—Sea temperatures fell to 10.5°C on 24 September after 7 consecutive days of 5–15 K northerlies. A shift to southerlies on 25 September started another climb, and the transition to the downwelling season clearly was under way. This transition, however, was not nearly so well defined as that which had introduced the upwelling season 6 months before.

10–20 m, which often limited visibility to a few meters. These diatom blooms were most evident during the intermittent episodes of downwelling. The benthos similarly proliferated. Within a few weeks after the initial upwelling, a growth of benthic diatoms (primarily *Isthmia nervosa* and *Tricertium americana*) appeared on the previously baron rocks, and even on sand sheltered from wave surge. Then larger elements of the biota began to increase in size and number. Particularly evident were calcareous sponges (especially *Leucosolenia* spp.), hydroids, and certain bryozoans. Benthic algae, predominantly *Desmarestia ligulata*, rapidly overgrew much of the rock substrata, while young *Nereocystis leutkeana*, which first appeared on the seafloor in May, had grown to the water's surface by mid-June. Swarms of mysids were increasingly numerous near the seafloor in April (they had been prominent for a month or more), and caprellid and gammaridean amphipods on rocky substrata began a sharp increase in numbers.

The bull kelp had formed a dense canopy by mid-July, and at about the same time large numbers of sori (reproductive structures) began falling from the kelp's fronds. (A frond that had recently lost a sorus appears at the left side of Figure 1.) Planktonic diatoms continued to proliferate during periodic blooms, but by this time the benthic diatoms that had carpeted much of the seafloor during the spring were mostly gone. Similarly, the mysid swarms, which had peaked in May and June, usually began to decline by mid-July. Other elements of the biota,

TABLE 2.—Food of adult *Sebastes mystinus* relative to near-surface plankton during upwelling episodes of the upwelling season. $n = 7$.

	Food organism	In diet				In plankton			
Rank	Taxa (rank index)	Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
1	PLANTS (3751.20)	NR[2]	72	NR	52.1	NR	NR	NR	NR
	Nereocystis sori	15–20	15	1.10	10.6	NR	NR	NR	NR
	Porphyra sp.	NR	15	NR	9.9	NR	NR	NR	NR
	Smithora naidum	NR	21	NR	17.0	NR	NR	NR	NR
	Others	NR	21	NR	14.6	NR	NR	NR	NR
2	PELAGIC HYDROZOA (1373.30)	10–30	21	4.51	14.5	<1–4	86	120.08	2.3
	Hydromedusae								
	Eutonina indicans	—	0	0.00	0.0	—	0	0.00	0.0
	Others	—	0	0.00	0.0	<1–2	86	68.65	0.6
	Syphonophora								
	Muggiaea atlantica	—	0	0.00	0.0	—	0	0.00	0.0
	Stephanomia bijuga	—	0	0.00	0.0	—	0	0.00	0.0
	Others	—	0	0.00	0.0	3–4	14	51.43	1.7
	Chondrophora								
	Velella velella	10–30	21	4.51	14.5	NA[3]	NA	NA	NA
3	MYSIDACEA (203.15)	5–7	3	10.26	6.6	—	0	0.00	0.0
	Acanthomysis spp.[4]	5–7	3	10.26	6.6	—	0	0.00	0.0
	Others	—	0	0.00	0.0	—	0	0.00	0.0
4	SCYPHOZOA (61.60)[5]	NR	8	NR	7.7	NR	NR	NR	NR
	Fragments	NR	8	NR	7.7	NR	NR	NR	NR
5	EUPHAUSIACEA (35.10)	5–8	15	1.95	1.2	<1–4	57	363.60	3.1
	Larvae	—	0	0.00	0.0	<1–4	57	363.60	3.1
	Thysanoessa spp.	5–8	15	1.95	1.2	—	0	0.00	0.0
	Others	—	0	0.00	0.0	—	0	0.00	0.0
6	GAMMARIDEA (1.80)	1–8	8	0.75	0.3	1–8	86	10.31	5.3
	Atylus tridens	—	0	0.00	0.0	2–8	29	4.63	5.0
	Ishyrocerus n. sp.	4	3	0.31	0.1	—	0	0.00	0.0
	Jassa falcata[6]	1–3	8	0.28	0.1	<1–3	14	0.78	NR
	Polycheria osbourni	—	0	0.00	0.0	—	0	0.00	0.0
	Others	2–8	5	0.16	0.1	1–2	57	4.90	0.3
7	CALANOIDA (0.90)	5–6	8	0.16	0.7	<1–7	100	2454.09	38.6
	Nauplii	—	0	0.00	0.0	<1	14	72.00	0.1
	Acartia spp.	—	0	0.00	0.0	1–2	52	224.23	4.4
	Calanus pacificus	—	0	0.00	0.0	2–3	57	24.68	5.3
	Eucalanus californicus	6	8	0.13	0.6	4–7	71	35.48	1.4
	Rhincalanus nasutus	—	0	0.00	0.0	—	0	0.00	0.0
	Others[7]	5	3	0.03	0.1	<1–3	1	2097.70	27.4

however, reached maximum development during the summer. Prominent among them were benthic algae, e.g., *Desmarestia ligulata* and *Laminaria setchelli*, as well as certain sedentary animals including various sponges, e.g., *Leucilla nuttingi*; ascidians, e.g., *Tridemnum opacum*; hydroids, e.g., *Obelia* spp.; and bryozoans, e.g., *Bugula* spp. The benthic caprellids and gammarideans attained peak numbers during early summer, when they literally carpeted some areas of the seafloor. Samples taken with an airlift during July 1978 measured densities of over 10,000 caprellids (mostly *Metacaprella kennerleyi*), and 108,000 gammarids (mostly *Jassa* spp.) in m^2 quadrats. Their numbers declined sharply during August, however, and by September they occurred only in scattered patches.

Feeding Conditions

The diet of *S. mystinus* relative to foods present during the upwelling season was assessed with samples of gut contents and near-surface plankton taken during 7 upwelling episodes (Table 2) and 10 downwelling episodes (Table 3).

More prey were consumed during the downwelling episodes (e.g., $\bar{x}$ no. prey taken = 110.8, vs. 20.1 during upwelling episodes). Thaliacians (Fig. 6) were the primary food during the upwelling season, but all were taken during downwelling episodes—the only times when the guts were packed with food. These relatively large, gelatinous zooplankters did not occur either in the plankton or in the diet of *S. mystinus* during upwelling episodes.

TABLE 2.—*Continued.*

Rank	Food organism: Taxa (rank index)	In diet: Size (mm)	In diet: % occur.	In diet: $\bar{x}$ no.	In diet: $\bar{x}$ % vol.	In plankton: Size (mm)	In plankton: % occur.	In plankton: $\bar{x}$ no.[1]	In plankton: $\bar{x}$ % vol.
8	**CAPRELLIDEA (0.54)**	**10**	**5**	**1.08**	**0.1**	**6**	**14**	**2.25**	**0.4**
	Metacaprella kennerlyi	10	5	1.08	0.1	—	0	0.00	0.0
	Others	—	0	0.00	0.0	6	14	2.25	0.4
9	**CHAETOGNATHA (0.09)**	**23**	**3**	**0.03**	**1.0**	**3–12**	**57**	**20.80**	**2.1**
	Undetermined species	23	3	0.03	1.0	3–12	57	20.80	2.1
10	**FISHES (0.02)**	**12**	**3**	**0.05**	**0.1**	**2–14**	**57**	**14.92**	**1.1**
	Larvae	12	3	0.05	0.1	2–14	57	14.92	1.1
OTHER CATEGORIES									
	Polychaeta	—	0	0.00	0.0	<1–12	86	74.83	1.4
	Molluscan larvae	—	0	0.00	0.0	<1–1	57	149.92	1.7
	Pelagic gastropoda	—	0	0.00	0.0	1–5	29	2.32	8.6
	Cladocera	—	0	0.00	0.0	1	29	64.28	0.7
	Harpacticoida	—	0	0.00	0.0	1–2	1	54.77	0.7
	Cyclopoidea	—	0	0.00	0.0	1	71	75.08	0.9
	Cirripedean larvae	—	0	0.00	0.0	<1–1	1	1850.92	15.0
	Reptantian larvae	—	0	0.00	0.0	<1–2	86	134.48	1.9
	Natantian larvae	—	0	0.00	0.0	2–3	43	72.00	1.4
	Larvacea	—	0	0.00	0.0	3–8	43	53.48	1.1
	Eggs, undetermined	—	0	0.00	0.0	<1	43	3024.00	9.7
	Eggs, fish	—	0	0.00	0.0	<1–2	71	312.68	1.7
UNIDENTIFIABLE MATERIAL[8]		—	—	—	15.9	—	—	—	—

No. fish examined: 51
224–336, $\bar{x}$ = 284.3 mm SL
No. empty = 13
$\bar{x}$ no. prey: individuals = 20.13
taxa = 2.03

No. plankton collections: 7
$\bar{x}$ no. zooplankters: 4940.57

[1]Value is estimated mean number per 100 m^3 of water, based on water filtered (54.8 m^3) during the 5-min collection.
[2]NR = not recorded. The enumeration was either omitted or unfeasible.
[3]*Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[4]Most mysids sampled were *Acanthomysis sculpta*.
[5]Adult *S. mystinus* often were seen feeding on large individuals of *Cyanea capillata* (Fig. 5), which were avoided by us during plankton collections because they would have made collections unmanageable.
[6]According to Kathleen Conlan (National Museum of Canada, P.O. Box 3443, Station D, Ottawa, Canada K1P 6P4, pers. commun. 26 May 1987), *Jassa falcata* does not occur in California, and forms along the coast considered to be this species (including the form(s) referred to here) are undescribed.
[7]Many of the calanoids from the plankton included in this category were juveniles and other undetermined stages of the species distinguished above. Most were at the lower end of the size range indicated.
[8]Foods digested beyond recognition.

FIGURE 5.—Adult *Sebastes mystinus* feeding on a scyphozoan, *Cyanea capillata*.

TABLE 3.—Food of adult *Sebastes mystinus* relative to near-surface plankton during downwelling episodes of the upwelling season. n = 10.

		In diet				In plankton			
Rank	Food organism Taxa (rank index)	Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
1	THALIACEA (124990.86)	**1–10**	**47**	**76.20**	**34.9**	**3–45**	**30**	**130.70**	**8.9**
	Undetermined species	1–10	47	76.20	34.9	3–45	30	130.70	8.9
2	PLANTS (2030.40)	**NR[2]**	**54**	**NR**	**37.6**	**NR**	**NR**	**NR**	**NR**
	Nereocystis sori	NR	18	NR	9.7	NR	NR	NR	NR
	Porphyra sp.	NR	22	NR	11.5	NR	NR	NR	NR
	Smithora naidum	NR	15	NR	5.5	NR	NR	NR	NR
	Others	NR	28	NR	10.9	NR	NR	NR	NR

TABLE 3.—*Continued.*

Rank	Food organism: Taxa (rank index)	In diet: Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	In plankton: Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
3	**CALANOIDA (778.78)**	**3–6**	**20**	**16.93**	**2.3**	**<1–8**	**100**	**5557.10**	**31.9**
	Nauplii	—	0	0.00	0.0	<1–1	50	594.00	1.8
	Acartia spp.	—	0	0.00	0.0	1–2	1	1121.00	4.6
	Calanus pacificus	—	0	0.00	0.0	2–5	70	105.84	2.4
	Eucalanus californicus	4–6	20	16.92	2.3	1–8	70	796.68	14.6
	Rhincalanus nasutus	—	0	0.00	0.0	5–6	10	92.88	2.7
	Others[3]	3	1	0.01	<0.1	<1–3	1	2846.70	5.8
4	**HYPERIIDEA (405.13)**	**2–13**	**49**	**6.36**	**1.3**	**1–7**	**60**	**17.10**	**0.6**
	Hyperoche medusarum	2–6	5	0.38	0.1	1–7	20	9.72	0.3
	Vibilia spp.	5	24	4.35	0.7	—	0	0	0
	Others	2–13	23	1.63	0.5	1–3	40	7.38	0.3
5	**PELAGIC GASTROPODA (334.66)**	**1–20**	**16**	**5.81**	**3.6**	**1–18**	**20**	**37.44**	**1.1**
	Heteropoda								
	Carinaria japonica	10–20	8	2.35	2.0	—	0	0.00	0.0
	Pteropoda								
	Corolla spectabilis	10–15	11	3.45	1.6	15–18	10	4.32	0.8
	Limacina helicina	3	1	0.01	<0.1	1–2	20	33.12	0.3
	Others	—	0	0.00	0.0	—	0	0.00	0.0
6	**PELAGIC HYDROZOA (318.24)**	**2–35**	**30**	**1.56**	**6.8**	**1–20**	**70**	**240.66**	**8.8**
	Hydromedusae								
	Eutonina indicans	—	0	0.00	0.0	10–20	10	0.54	0.3
	Others	—	0	0.00	0.0	1–5	50	187.56	5.8
	Syphonophora								
	Muggiaea atlantica	8–9	5	0.27	0.2	6–9	10	2.88	0.6
	Stephanomia bijuga	NR	5	0.31	0.2	—	0	0.00	0.0
	Others	2–16	14	0.51	2.7	2–6	20	49.68	2.1
	Chondrophora								
	Velella velella[4]	25–35	7	0.47	3.7	NA[4]	NA	NA	NA
7	**LARVACEA (1.12)**	**2–7**	**8**	**0.70**	**0.2**	**2–6**	**70**	**142.74**	**2.2**
	Undetermined	2–7	8	0.70	0.2	2–6	70	142.74	2.2
8	**POLYCHAETA (0.87)**	**4–25**	**19**	**0.46**	**0.1**	**<1–7**	**70**	**103.50**	**0.7**
	Larvae	—	0	0.00	0.0	<1–4	70	90.36	0.3
	Postlarvae	4–25	19	0.46	0.1	7	10	13.14	0.4
9	**FISHES (0.73)**	**8–45**	**4**	**0.14**	**1.3**	**2–11**	**50**	**4.50**	**0.4**
	Larvae	8–45	4	0.14	1.3	2–11	50	4.50	0.4
10	**SCYPHOZOA (0.02)**	**NR**	**3**	**0.01**	**0.5**	**NR**	**NR**	**NR**	**NR**
	Fragments	NR	3	0.01	0.5	NR	NR	NR	NR
OTHER CATEGORIES									
	Molluscan larvae	NR	1	0.01	<0.1	<<1–<1	70	631.08	4.9
	Cladocera	—	0	0.00	0.0	<<1–<1	40	115.92	1.7
	Harpacticoida	NR	3	0.03	NR	<1–2	70	55.25	1.1
	Cirripedean larvae	—	0	0.00	0.0	<1–2	100	1372.44	11.8
	Gammaridea	1–8	12	0.32	0.5	<1–3	90	12.24	0.6
	Euphausiacea	2–12	9	0.11	0.7	<1–11	60	229.86	1.0
	Reptantian larvae	—	0	0.00	0.0	<1–3	70	119.52	2.1
	Natantian larvae	—	0	0.00	0.0	1–6	60	43.20	0.7
	Chaetognatha	—	0	0.00	0.0	6–18	50	18.54	1.2
	Eggs, undetermined	NR	12	0.74	0.3	<<1–<1	50	2921.40	5.0
	Eggs, fish	—	0	0.00	0.0	<1–2	60	48.96	0.9
UNIDENTIFIABLE MATERIAL[5]		—	—	—	11.0	—	—	—	—

No. fish examined: 85
204–335, $\bar{x}$ = 266.2 mm SL
No. empty = 8
$\bar{x}$ no. prey: individuals = 110.84
taxa = 3.35

No. plankton collections: 10
$\bar{x}$ no. zooplankters: 6622.50

[1]Value is estimated mean number per 100 m³ of water, based on water filtered (54.8 m³) during the 5-min collection.
[2]NR = not recorded. The enumeration was either omitted or unfeasible.
[3]Many of the calanoids from the plankton included in this category were juveniles and other undetermined stages of the species distinguished above. Most were at the lower end of the size range indicated.
[4]*Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[5]Foods digested beyond recognition.

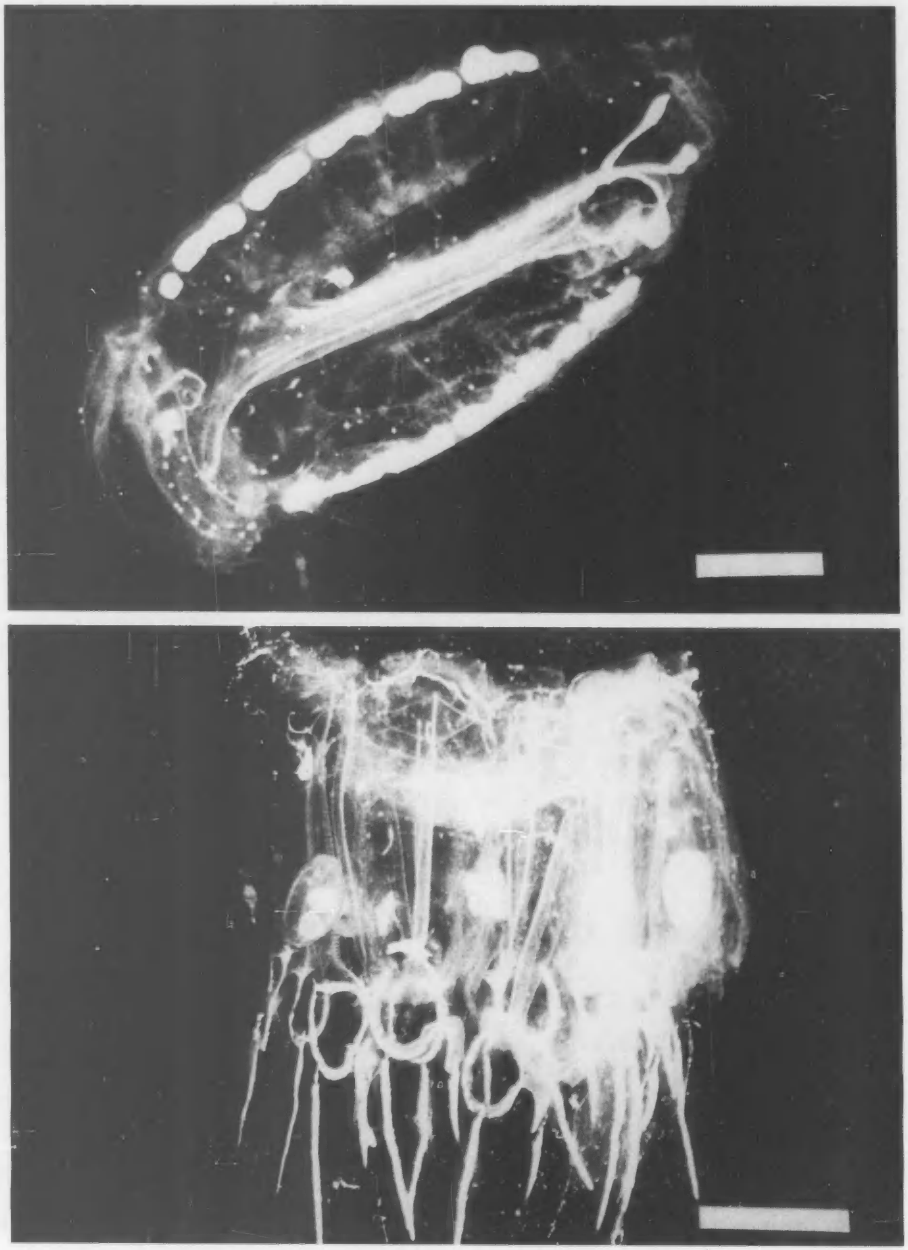

FIGURE 6.—Thaliacean, *Cyclosalpa bakeri*, off Mendocino. Solitary individual (upper) and aggregate of individuals (below). Scale indicator = 1 cm.

Plant material ranked as the top food-category during upwelling episodes (Table 2) and as the second-ranked food during downwelling episodes (Table 3). In both cases, certain algae dominated the diet on days when offshore zooplankters were in short supply during the latter part of the upwelling season (upwelling episodes on 8 August 1978, 12 June 1979, and 17 June 1981; downwelling episodes on 24 July 1979 and 27 August 1979; see Table 1). Algae were not taken earlier in the season, however. Thus, while the six individuals collected during a plankton-poor upwelling episode of 8 August 1978 (Table 1) were full of algae (90% of gut contents) and epibenthic crustaceans (10%), all eight collected during a plankton-poor upwelling episode of 9 April 1981 (Table 1) were empty. Similarly, the occurrence of algae in the diet during downwelling episodes (Table 3) is based mostly on 20 adults collected during two days (24 and 27 August 1979) when environmental conditions indicated downwelling but an absence of offshore zooplankters was noted (Table 1). There was no indication of plants being ingested for epiphytic animals.

Of the wide variety of plant materials in the diet, only the three most frequently ingested forms appeared to some extent digested. These were the sori of *N. leutkeana*, *Porphyra nereocystis* (an epiphyte on *N. leutkeana*), and *Smithora naidum* (an epiphyte on certain seagrasses). The sori of *N. leutkeana* developed as variably sized areas (typically about 50–150 mm long) in fronds near the water's surface. They dropped from the fronds when mature, and we saw several ingested by *S. mystinus* as they drifted toward the bottom. Sori recovered from the intestines of *S. mystinus* were more translucent than sori from the stomach, but comparison under magnification of sectioned material from both regions of the gut (Fig. 7) indicated that only zoospores were digested. Ingested fragments of *P. nereocystis* and *S. naidum*, both species having monostromatic thalli, ranged from intact, but flaccid and blanched, to disintegrating. Ingested *S. naidum* often were attached to pieces of *Zostera marina* or *Phyllospadix torreyi*, but these seagrasses never evidenced digestion. Nor did other plant forms present among the gut contents appear to be digested, including *D. ligulata* and *N. leutkeana* (vegetative tissue), along with various unidentified phaeophytes and rhodophytes. Thus, plants contributed less food than is indicated by the tables and histograms, where their rank is inflated by undigested materials.

Zooplankters taken during upwelling episodes differed from early to late in the season, whereas those taken during downwelling episodes remained much the same throughout (as listed in Table 3). Thus, of the food categories listed for the upwelling condition (Table 2), pelagic hydrozoans, mysids, and scyphozoans were taken only during the spring, whereas euphausiids and caprellids were taken only in summer. The only notable departure from the downwelling condition depicted in Table 3 occurred on 24 April 1979 (Table 1), when conditions were at the time judged to be mixed. Upwelling had been unusually weak during the first month of that upwelling season, and there was no wind at the time of sampling. The sea was calm and, at 10°C, warm for April. Although these conditions usually indicate downwelling (which is why the data are assigned to that category), we neither collected nor saw organisms typical of downwelling conditions. Furthermore, of the nine adult *S. mystinus* (224–313, $\bar{x}$ = 277.7 mm SL) collected, eight (89%) were empty. The ninth contained one sorus from *N. leutkeana* (an unusually large number of *N. leutkeana* had persisted through the previous winter, which had been exceptionally mild) and also organisms not seen or collected by us in the environment at the time: two *Corolla spectabilis* (a pelagic gastropod typical of downwelling conditions) and six *Velella velella* (a pelagic hydrozoan typical of upwelling conditions). The latter float on the water's surface (Fig. 8), and often we saw adult *S. mystinus* break the surface to feed on them.

The Downwelling Season

Between late August and mid-September it became evident that transition to the downwelling season was under way. Winds had become light and variable (but generally remained either northerly or southerly), and for a growing number of days at a time, the water was notably blue and transparent. Records of sea temperatures and wind for the 1980–81 downwelling season illustrate how occurrences of downwelling and upwelling related to prevailing wind during that period (Fig. 9).

Habitat Conditions

The downwelling season developed with less wind from the north and more wind from the south, but either way with winds that tended to be light, so that relatively tranquil conditions prevailed. Flowing into the nearshore habitat with offshore surface waters was a rich supply of relatively large, mostly gelatinous zooplankters that were major prey of *S.*

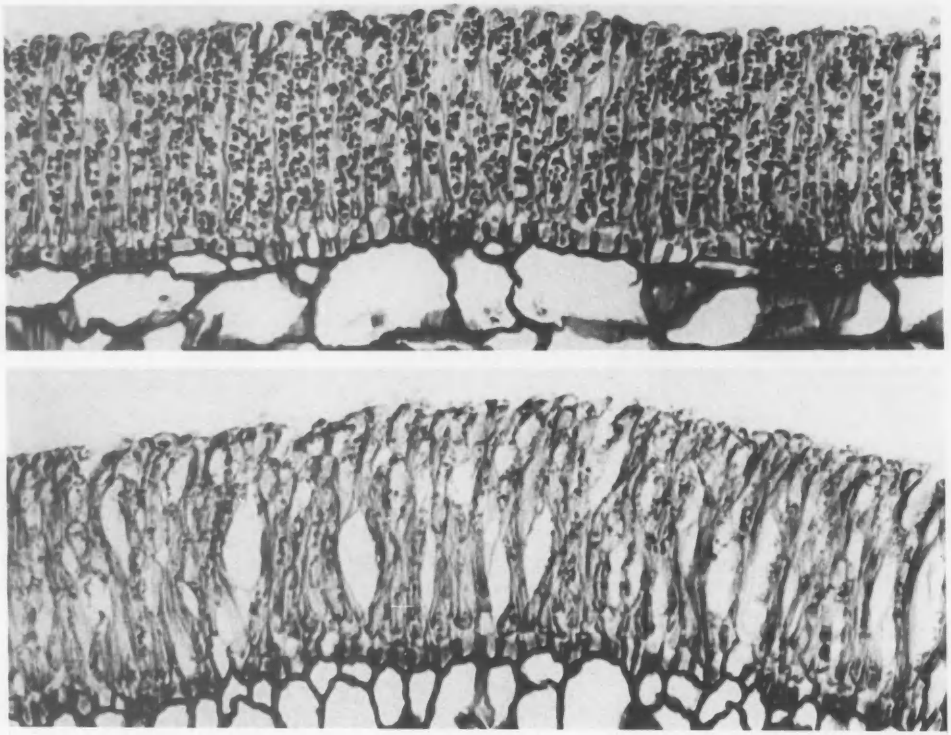

FIGURE 7.—Sections through surface region of sori (stained with hematoxylin) from gut of *Sebastes mystinus*. Upper section is from the stomach, lower is from the intestine. Granular objects in upper section but largely absent in lower section are zoospores in zoosporangia.

mystinus. But, whereas the predominant of such forms during spring and summer usually were thaliaceans, during the fall they were usually ctenophores (Fig. 10), pelagic hydrozoans—mostly siphonophores (Fig. 11), and hydromedusae. The pelagic hydrozoan *Velella velella*, which had been prominent during the upwelling season, was not seen. Pelagic gastropods (Fig. 12), pteropods at least, also were more abundant during fall downwelling. On the other hand, these waters were poor in the pelagic diatoms that had bloomed periodically during spring and summer. Furthermore, the nearshore habitat had by this time lost much of its benthos. Many of the more insecurely anchored *Nereocystis* plants, for example, had been carried away by strong wave surge that frequently swept through the nearshore habitat even during relatively tranquil periods. Although the loss of these plants greatly increased interplant distances, *Nereocystis* beds remained dominant features. This was because the plants still in place continued to grow, to produce sori, and to thicken the surface canopy. Probably at least partly because the canopy's increased thickness blocked sunlight from the seafloor below, the algal understory, *Desmarestia lingulata* in particular, was greatly reduced. Similarly, many benthic animals that proliferated during the previous upwelling season had become scarce, including the amphipods and mysids noted above to be declining during late summer.

As the downwelling season progressed through fall toward winter, there were major transformations of the nearshore habitat that, to at least some extent, resulted from southwesterly storms. The

FIGURE 8.—*Velella velella* being driven shoreward by a northwest wind off the coast of northern California.

major effects of storms on the nearshore habitats came from 1) physical force of waves and surge, and 2) suspended sediments carried by coastal runoff into the nearshore habitats after heavy rains. The first of these was the more apparent, at least in exposed locations where often many of the benthic algae and sessile invertebrates were swept away. This force, intensified when the water carried abrasive sediments, swept away most of the *Nereocystis*, although some plants survived the winter in sheltered places where they continued to produce sori. Suspended sediments had their most obvious effects in locations sheltered from water movement, where they frequently settled to blanket the benthos. Probably a more profound effect of materials in suspension, however, was reduced transparency of the water that limited the amount of light (already at low levels owing to the shorter days and low sun angle) reaching phototrophic organisms.

As a general result of these, and probably other forces in combination, the nearshore habitat appeared relatively barren during the latter stages of the downwelling season. That storms were a major factor in reducing the vitality of this habitat was apparent during the relatively mild winter of 1978–79, when the effects described above were reduced. That was the only year, for example, when mysids were noted to be conspicuous in the nearshore habitat throughout the winter.

Feeding Conditions

The diet of *S. mystinus* relative to foods available during the downwelling season was assessed during 10 days of sampling under downwelling condi-

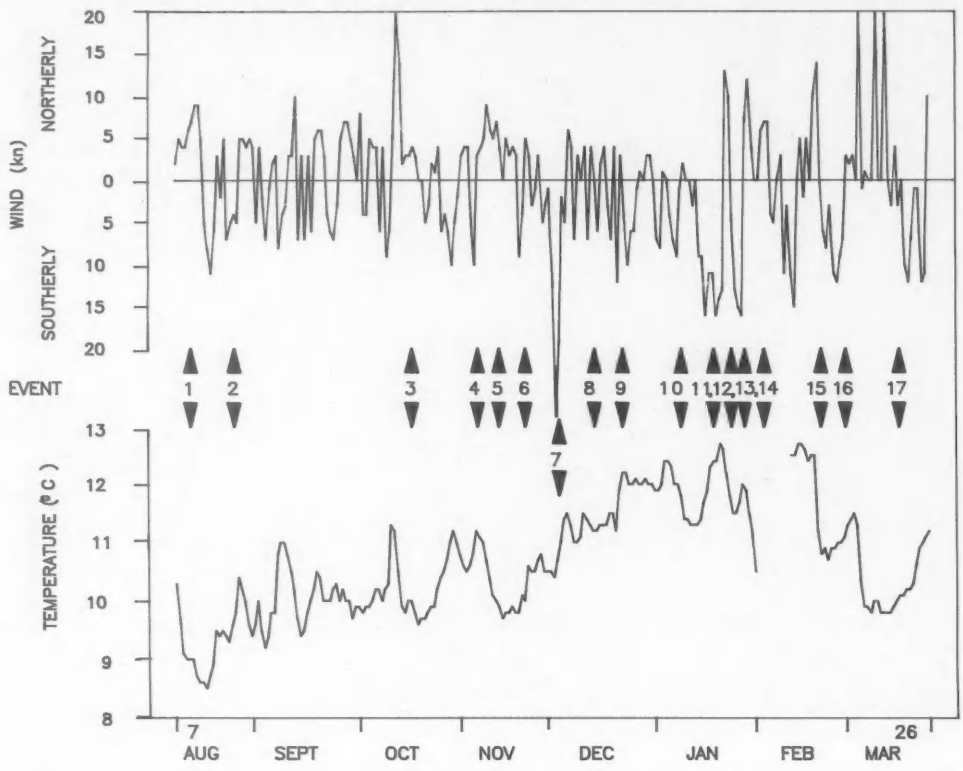

FIGURE 9.—Sea temperatures and wind off Mendocino during the 1980–81 downwelling season. See capture of Figure 4 and text for methods used in obtaining and plotting the data.

EVENT 1—Sea temperature fell to 8.5°C on 16 August after 9 consecutive days of 7–10 K northerlies, producing the last episode of strong upwelling during the 1980 upwelling season.

EVENT 2—Sea temperature rose to 10.4°C on 26 August after southerlies of 5–12 K on 9 of the preceding 11 days. Then began a 6-wk transition to the downwelling season, during which 1–4 day periods of 2–10 K northerlies, with slightly lowered sea temperatures, alternated with 1–4 day periods of southerlies, with slightly elevated temperatures.

EVENT 3—The last bit of upwelling before the season's first major downwelling episode began on 14 October with 7 consecutive days of northerlies—20 K during the first 2, 4–8 K during the next 5.

EVENT 4—Sea temperatures rose to 11.2°C on 7 November after 16 straight days of 2–12 K southerlies or weak (2–5 K) northerlies.

EVENT 5—Sea temperatures fell to 9.7°C during a major cooling that coincided with 8 days of 3–9 K northerlies (with gusts to 20 K) from 8 to 15 November.

EVENT 6—On 21 November the wind shifted to the south, with gusts to 20K, and sea temperatures began rising.

EVENT 7—A 3-day storm (1–3 December) with 20–30 K southerlies (and rain) briefly accelerated the rise in temperature.

EVENT 8—The warming trend was briefly interrupted by several 1–3 day periods of 4–10 K northerlies.

EVENT 9—By 22 December sea temperatures had risen to levels above 12°C that characterized the 1980–81 downwelling season. Although southerlies predominated over the next 3 weeks, on some days reaching 25 K (e.g., on 25 December), there were no further large increases in temperature.

EVENT 10—Sea temperatures anomalously fell during the first 2 weeks of January, even though winds during that period were mostly southerlies of up to 10 K.

EVENT 11—An 8-day storm (15–22 January) with 12–20 K southerlies (and rain) resulted in sea temperatures rising to 12.7°C—the warmest of the year (equaled 3 weeks later).

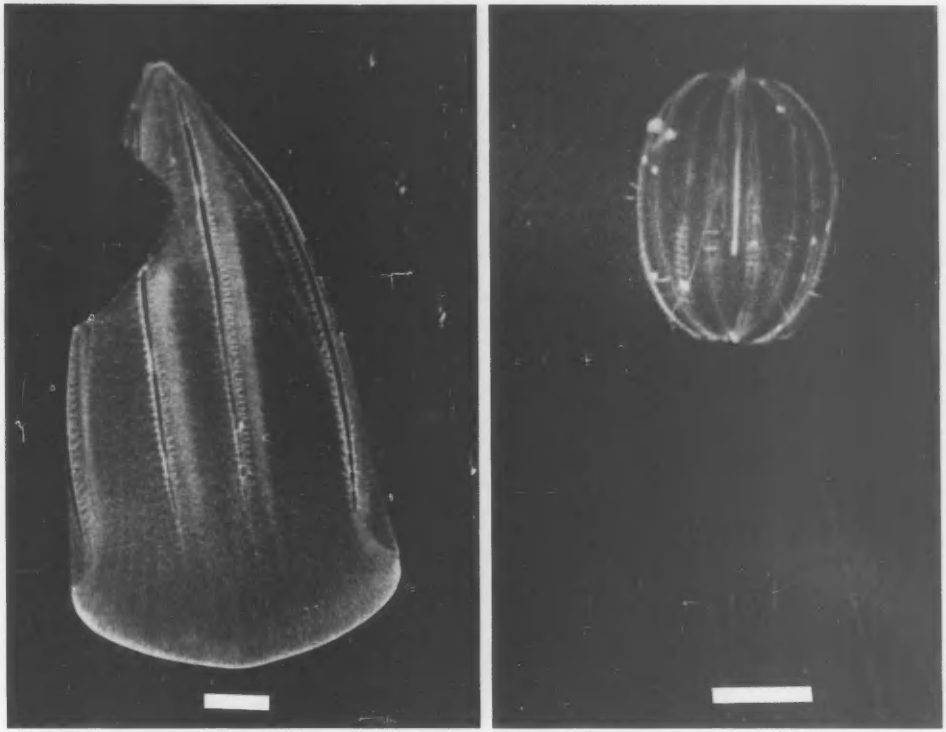

FIGURE 10.—Ctenophores off Mendocino. *Beroe forskali* (left), missing piece probably taken by planktivore, and *Pleurobrachia bachei* (right). Scale indicator = 1 cm.

EVENT 12—The process abruptly reversed with a shift to northerlies that gusted to 30 K for 2 days, and sea temperature fell to 11.5°C on 25 January.

EVENT 13—In another abrupt reversal, 3 days (27–29 January) of 15–25 K southerlies (with rain) resulted in sea temperature rising to 12°C.

EVENT 14—Reversing again, northerlies of 12–20 K on 30–31 January drove sea temperatures down to 10.5°C, at which point (1 February) the thermograph malfunctioned. Southerlies predominated while the thermograph was inoperative, and when it was reinstalled on 11 February, rising sea temperature 2 days later (13 February) equaled the season high of 12.5°C. But when northerlies returned the next day the downwelling season began its decline.

EVENT 15—Two days of 20–25 K northerlies (19–20 February) resulted in the season's largest 24-h change in sea temperatures.

EVENT 16—Sea temperature rose to 11.5°C on 3 March following 8 consecutive days of 8–15 K southerlies (with rain), or weak northerlies (to 6 K). An abrupt shift followed, as 2 days of 15–25 K northerlies (4–5 March) resulted in the season's second largest 24-h change in sea temperature—the first time since November that sea temperature had fallen below 10°C.

EVENT 17—After a week of light variable winds, during which sea temperatures remained essentially unchanged at about 9.8°C, southerlies increased to 15–20 K (on 15 March) and sea temperatures began rising to begin the final downwelling episode of the 1980–81 downwelling season (which was followed by the abrupt reversal that marked the beginning of the 1981 upwelling season, see Figure 4).

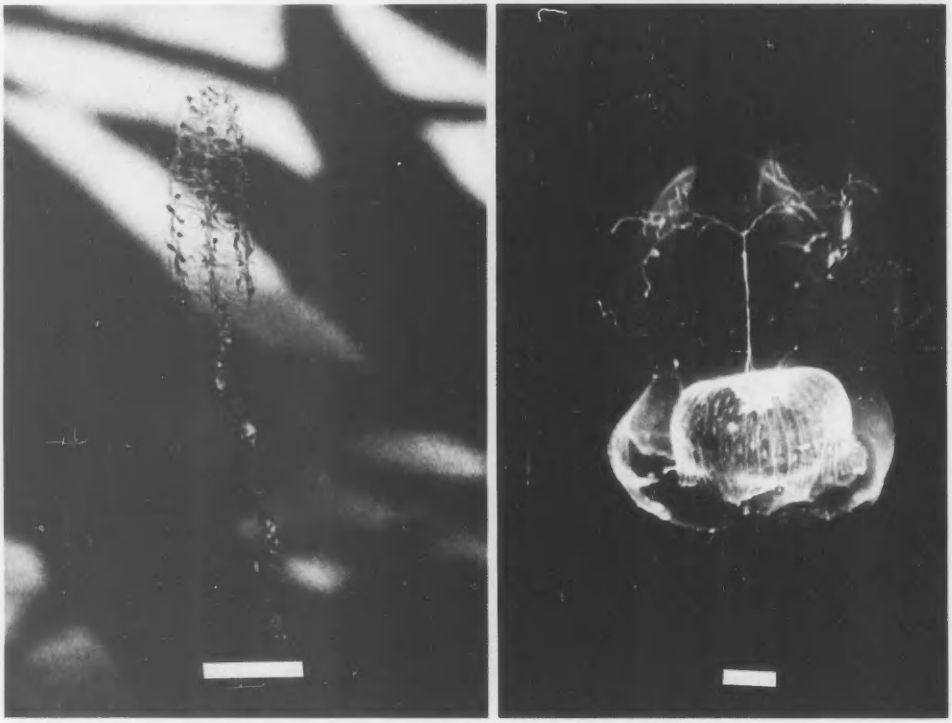

FIGURE 11.—Siphonophores off Mendocino. The physonect *Stephanomia bijuga* (left), and the calycophore *Praya dubia* (right). Scale indicator = 1 cm.

tions, but because fall and winter were so different, we consider them separately. We did not observe upwelling conditions during this period.

The major foods during six days of fall downwelling, based on the ranking indices (Table 4), were pelagic hydrozoans, specifically siphonophores, but vegetation comprised a larger part of the total diet volume. Virtually all plant materials taken at these times, however, were sori of *N. leutkeana*. As was true during the upwelling season, there tended to be more vegetation in the diet when there were fewer of the larger gelatinous zooplankters in the water column. For example, during the sampling session of 18 October 1978 (Table 1), when the surface plankton-collections took 400 siphonophores and ctenophores, only 1 of the 9 fish collected had consumed plant material (one sorus of *N. leutkeana*). On the other hand, during the sampling session of 16 October 1979 (Table 1), when the surface plankton-collection took only 30 siphonophores and ctenophores, 10 of 13 fish collected had consumed vegetation ($\bar{x}$ diet volume = 80%, virtually all of it sori of *N. leutkeana*; number taken = 1–21, $\bar{x}$ = 9.0), and two others were empty.

Our assessment of the diet and concurrent composition of the plankton during winter downwelling is limited to four days of sampling (Table 5). Data from these collections are combined for consistency

FIGURE 12.—Pelagic gastropods off Mendocino. The heteropod *Carinaria japonica* (upper), and the pteropod *Corolla spectabilis* (lower). Scale indicator = 1 cm. Often in areas where blue rockfish are feeding many of the *C. spectabilis* present have lost the bulbous central part of their body (pseudoconch and viscera).

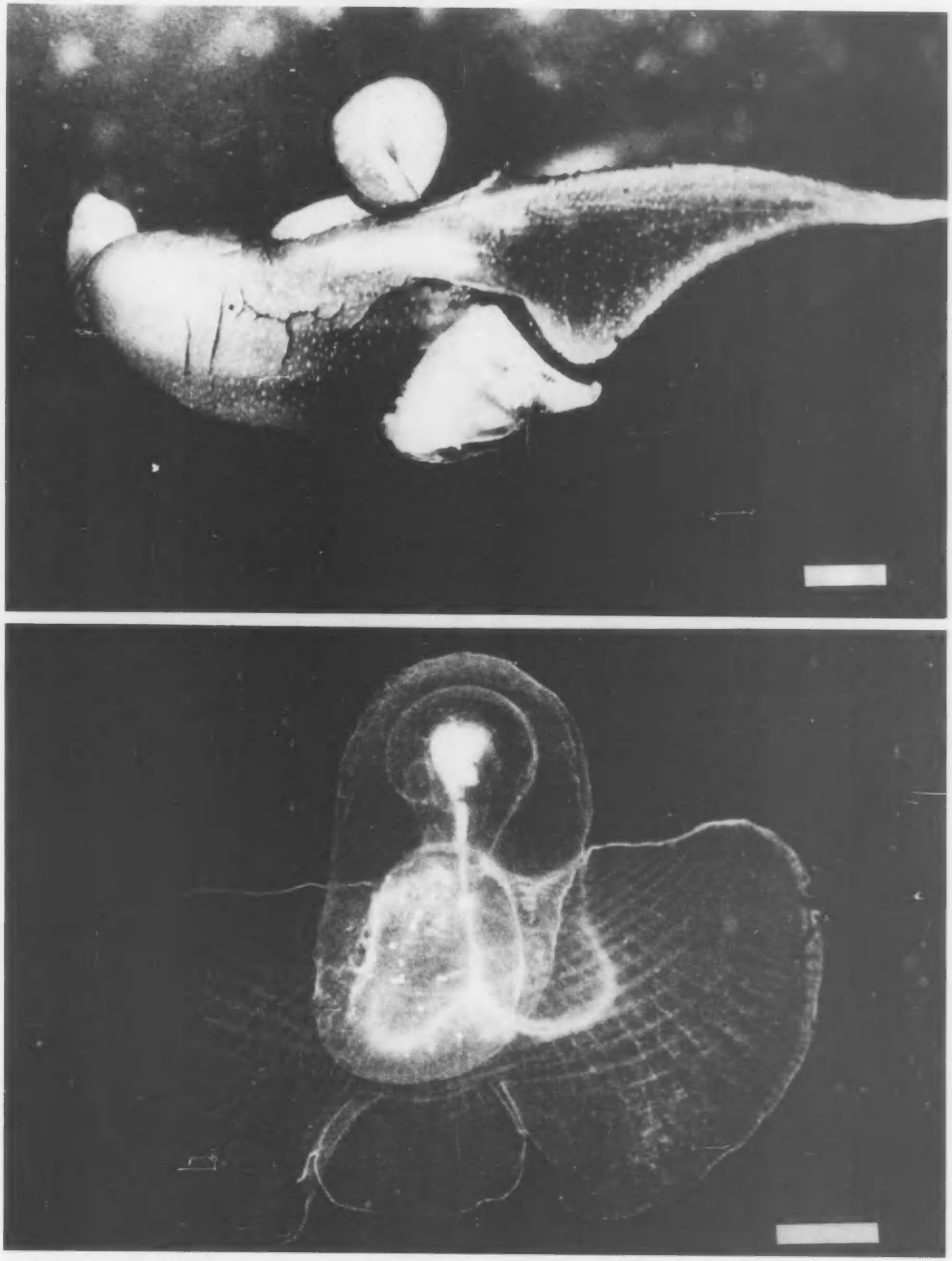

TABLE 4.—Food of adult *Sebastes mystinus* relative to near-surface plankton during downwelling episodes of fall. n = 6.

	Food organism	In diet				In plankton			
Rank	Taxa (rank index)	Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
1	**PELAGIC HYDROZOA (10455.98)**	**2–15**	**46**	**18.04**	**12.5**	**1–25**	**83**	**1747.12**	**26.5**
	Hydromedusae								
	Eutonina indicans	18	1	0.03	<0.1	18–25	33	1516.81	14.7
	Others	15	4	0.02	<0.1	<1–20	33	26.10	0.2
	Syphonophora								
	Muggiaea atlantica	6–15	10	0.34	0.7	5–12	67	15.83	2.0
	Stephanomia bijuga	10	17	1.33	0.8	10	17	2.39	0.3
	Others	2–15	31	16.32	10.9	1–8	4	185.99	9.3
	Chondrophora								
	Velella velella[2]	—	0	0.00	0.0	NA[2]	NA	NA	NR
2	**PLANTS (4123.00)**	**NR[3]**	**54**	**2.06**	**37.1**	**NR**	**NR**	**NR**	**NR**
	Nereocystis sori	NR	51	1.94	35.6	NR	NR	NR	NR
	Porphyra sp.	NR	2	NR	0.2	NR	NR	NR	NR
	Smithora naidum	NR	6	0.06	<0.1	NR	NR	NR	NR
	Others	NR	6	0.06	1.3	NR	NR	NR	NR
3	**CTENOPHORA (1742.66)**	**3–15**	**33**	**5.74**	**9.2**	**<1–10**	**0.67**	**295.79**	**5.4**
	Pleurobrachia bachei	3–15	31	5.73	9.2	<1–10	50	288.59	5.2
	Others	12	1	0.01	<0.1	3	17	7.20	0.2
4	**PELAGIC GASTROPODA (554.00)**	**2–160**	**25**	**3.20**	**6.8**	**<1–45**	**100**	**187.82**	**8.4**
	Heteropoda								
	Caranaria japonica	12–160	15	0.33	2.1	30–45	17	1.21	0.7
	Pteropoda								
	Corolla spectabilis	5–22	16	2.69	4.7	2–20	50	72.90	7.5
	Limacina helicina	2	1	0.18	<0.1	1–3	17	109.80	0.2
	Others	—	0	0.00	0.0	<1–3	17	3.91	<0.1
5	**SCYPHOZOA (89.96)**	**10–35**	**18**	**0.51**	**9.8**	**NA**	**NA**	**NA**	**NA**
	Fragments	10–35	18	0.51	9.8	NA	NA	NA	NA
6	**THALIACEA (31.97)**	**5–29**	**16**	**0.54**	**3.7**	**2–5**	**17**	**3.01**	**NR**
	Undetermined species	5–29	16	0.54	3.7	2–5	17	3.01	NR
7	**EUPHAUSIACEA (22.93)**	**4–10**	**21**	**0.78**	**1.4**	**<1–9**	**67**	**162.90**	**2.2**
	Larvae	4	1	0.01	<0.1	4	50	129.01	1.2
	Thysanoessa spp.	4–10	19	0.74	1.4	5–9	33	33.89	1.0
	Others	8	1	0.03	<0.1	—	0	0.00	0.0

with the other tables and figures, but the combinations obscure the great variation in feeding conditions at this time of year. For example, taxa of the major food categories listed in Table 5 were numerous in the diet and plankton only during the two sampling sessions in February and March of 1979. Of the 14 fish collected at those times, all but one was well fed ($\bar{x}$ no. prey = 26.7), with the exception being a pregnant female whose gut was empty. Thaliaceans dominated on these occasions, both in the diet and in the plankton, and hyperiid amphipods, *Vibilia* spp. (which are parasites of thaliaceans (Laval 1980)), were similarly abundant. In contrast, the collecting session of January 1980 indicated there were more zooplankters in the water column, but that they were exceptionally small. The plankton collection took 1,488 zooplankters (compared with 109 and 715 in the two 1979 collections), but only 2% were of species that occurred as large as 2 mm (compared with 86% in 1979). That these small zooplankters were unsuitable as prey of adult *S. mystinus* is implicit in the fact that of 16 fish collected, only 3 contained food—all of it the alga *Porphyra* sp. (The other 13 represented 76% of all fish with empty guts in the winter collections.) Significantly, of the taxa identified as food of adult *S. mystinus* during the winter (Table 5), only one, the calanoid *Calanus pacificus*, was represented in the January 1980 plankton collection. Conditions were intermediate during the sampling session of January 1981, when some of the listed food taxa occurred in both diet and plankton (though in reduced numbers) and five of eight fish sampled contained food.

TABLE 4.—*Continued.*

Rank	Food organism: Taxa (rank index)	In diet: Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	In plankton: Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
8	**CALANOIDA (14.32)**	**2–7**	**22**	**0.93**	**0.7**	**<1–7**	**100**	**9528.11**	**28.3**
	Nauplii	—	0	0.00	0.0	<1–1	33	68.99	<0.1
	Acartia spp.	—	0	0.00	0.0	<1–1	83	1751.42	4.3
	Calanus pacificus	3	6	0.13	<0.1	<1–4	83	4609.21	15.8
	Eucalanus californicus	4–7	15	0.67	0.7	2–7	100	255.39	1.2
	Rhincalanus nasutus	4	4	0.06	<0.1	—	0	0.00	0.0
	Others[4]	2–3	3	0.07	<0.1	<1–3	100	2843.10	7.0
9	**HYPERIIDEA (8.28)**	**1–8**	**24**	**1.15**	**0.4**	**1–7**	**83**	**292.19**	**0.4**
	Hyperoche medusarum	2	3	0.16	0.1	1–7	50	273.01	0.2
	Vibilia spp.	—	0	0.00	0.0	—	0	0.00	0.0
	Others	1–8	21	0.99	0.3	1–3	33	19.18	0.2
10	**POLYCHAETA (3.20)**	**4–40**	**16**	**0.40**	**0.5**	**<1–7**	**83**	**118.21**	**1.7**
	Larvae	—	0	0.00	0.0	<1–4	33	103.81	1.5
	Postlarvae	4–40	16	0.40	0.5	3–7	50	14.40	0.2
OTHER CATEGORIES									
	Molluscan larvae	—	0	0.00	0.0	<<1–<1	50	189.59	0.7
	Cladocera	—	0	0.00	0.0	<1–1	33	142.20	0.8
	Cyclopoida	NR	1	0.01	NR	<1–1	67	648.00	4.0
	Cirripedean larvae	—	0	0.00	0.0	<<1–<1	67	128.70	0.2
	Reptantian larvae	—	0	0.00	0.0	<1–6	83	52.20	0.3
	Natantian larvae	—	0	0.00	0.0	1–5	33	237.60	NR
	Bryozoan larvae	—	0	0.00	0.0	<1	33	244.49	0.2
	Larvacea	2	3	0.12	0.1	<1–4	67	844.20	2.8
	Chaetognatha	10–11	3	0.06	0.2	5–20	83	225.59	5.0
	Eggs, undetermined	—	0	0.00	0.0	<1	17	1535.99	4.3
	Eggs, fish	3	1	0.01	<0.1	<1–2	33	40.19	4.4
	Fishes	6–24	4	0.04	0.2	4–20	33	5.40	0.7
UNIDENTIFIABLE MATERIAL[5]		—	—	—	17.4	—	—	—	—

No. fish examined: 73
218–350, $\bar{x}$ = 290.3 mm SL
No. empty = 7
$\bar{x}$ no. prey: individuals = 32.4
taxa = 3.6

No. plankton collections: 6
$\bar{x}$ no. zooplankters: 9663.0

[1]Value is estimated mean number per 100 m³ of water, based on water filtered (54.8 m³) during the 5-min collection.
[2]*Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[3]NR = not recorded. The enumeration was either omitted or unfeasible.
[4]Many of the calanoids from the plankton included in this category were juveniles and other undetermined stages of the species distinguished above. Most were at the lower end of the size range indicated.
[5]Digested beyond recognition.

DISCUSSION

It is clear that wind-driven movement of the surface water profoundly influences feeding by *Sebastes mystinus* off northern California. Water set in motion by the wind can be tens of meters deep (Bakun 1973; Barber and Smith 1981), and so carries most of the foods of nearshore planktivores. The movement is seaward (with upwelling) under northerly winds and shoreward (with downwelling) under southerly winds. Thus, with winds along the Mendocino coast being northerly or southerly about 80% of the time (based on records of the NOAA weather station there), adult *S. mystinus* in that area alternate between periods when planktonic foods are being carried into their habitat and periods when these foods are being carried away.

This perception of alternations between upwelling and downwelling is simplified, perhaps overly so, to emphasize features we consider essential to the feeding of *S. mystinus*, and also because details of what clearly is a complex oceanographic system remain unclear. In particular, we stress the importance of shoreward surface transport in carrying prey to *S. mystinus* in nearshore habitats. The major prey of adult *S. mystinus*—thaliaceans, pelagic hydrozoans, and other relatively large, gelatinous zooplankters—tend to be concentrated in areas of oceanic convergence, and dispersed in areas of oceanic divergence (e.g., Bakun and Parrish 1980). Thus, when offshore surface waters converge on the coast, the planktonic foods of *S. mystinus* become concentrated near shore.

TABLE 5.—Food of adult *Sebastes mystinus* relative to near-surface plankton during downwelling episodes of winter. $n = 4$.

	Food organism	In diet				In plankton			
Rank	Taxa (rank index)	Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
1	THALIACEA (29034.03)	**7–20**	**71**	**12.90**	**31.7**	**5–45**	**50**	**9.90**	**34.8**
	Undetermined species	7–20	71	12.90	31.7	5–45	50	9.90	34.8
2	HYPERIIDEA (3278.81)	**1–5**	**62**	**23.40**	**2.2**	**1–6**	**75**	**2.25**	**0.8**
	Hyperoche medusarum	—	0	0.00	0.0	4	25	0.45	NR[3]
	Vibilia spp.	1–5	57	23.06	2.1	5–6	25	0.90	0.8
	Others	6	5	0.34	0.1	1	25	0.90	NR
3	EUPHAUSIACEA (1567.61)	**6–12**	**43**	**11.76**	**3.1**	**10**	**75**	**2.25**	**12.5**
	Larvae	—	0	0.00	0.0	—	0	0.00	0.0
	Thysanoessa spp.	6–12	38	11.67	3.1	10	75	2.25	12.5
	Others	6	5	0.09	<0.1	—	0	0.00	0.0
4	SCYPHOZOA (1054.20)	**NR**	**38**	**1.43**	**19.4**	**NR**	**NR**	**NR**	**NR**
	Fragments[2]	NR	38	1.43	19.4	NR	NR	NR	NR
5	PELAGIC GASTROPODA (726.34)	**6–30**	**48**	**2.91**	**5.2**	**1–20**	**25**	**8.10**	**0.8**
	Heteropoda								
	Caranaria japonica	15–30	10	0.24	0.5	—	0	0.00	0.0
	Pteropoda								
	Corolla spectabilis	6–20	48	2.67	4.7	20	25	0.45	0.8
	Limacina helicina	—	0	0.00	0.0	1–2	25	7.65	NR
	Others	—	0	0.00	0.0	—	0	0.00	0.0
6	PELAGIC HYDROZOA (437.91)	**3–13**	**43**	**1.52**	**6.7**	**1–6**	**75**	**14.85**	**1.3**
	Hydromedusae								
	Eutonina indicans	—	0	0.00	0.0	—	0	0.00	0.0
	Others	10–22	40	0.33	3.5	1–4	50	12.60	0.5
	Syphonophora								
	Muggiaea atlantica	8–13	38	0.86	2.1	6	50	1.35	0.8
	Stephanomia bijuga	—	0	0.00	0.0	—	0	0.00	0.0
	Others	3–20	19	0.33	1.1	3	25	0.90	NR
	Chondrophora								
	Velella velella	—	0	0.00	0.0	NA[4]	NA	NA	NA
7	PLANTS (380.00)	**NR**	**38**	**NR**	**10.0**	**NR**	**NR**	**NR**	**NR**
	Nereocystis sori	NR	5	0.10	0.1	NR	NR	NR	NR
	Porphyra sp.	NR	19	NR	5.2	NR	NR	NR	NR
	Smithora naidum	—	0	0.00	0.0	NR	NR	NR	NR
	Others	NR	19	NR	4.7	NR	NR	NR	NR

Shoreward transport can be either wind-driven (Ekman transport), or result simply from relaxation of the forces that drive upwelling. But in either case our observations indicate that shoreward flowing surface waters override the colder waters near shore, a process we refer to as downwelling. Usually the term downwelling is limited to conditions that result from shoreward Ekman transport (e.g., Gross 1977), but we have found that relaxation of upwelling has essentially the same effect on the nearshore ecosystem, the difference being simply in degree of effect.

Some studies have concluded that warming of the nearshore surface waters during relaxation of upwelling results from alongshore advection (e.g., Send et al. 1987), but even though zooplankters entering our study area during downwelling generally moved southward along the coast, the characteristic presence of such forms as thaliaceans, ctenophores, and pteropods indicate that the advection is from offshore. So despite the complexities of circulation and mixing that occur in the coastal waters off northern California (e.g., Winant et al. 1987), the net result affecting the trophic relations of *S. mystinus* are alternations between seaward and shoreward transport.

These water movements follow a strong seasonal pattern that is evident in upwelling indices for lat. 39°N (which crosses Mendocino) produced by the Pacific Fisheries Environmental Group of the Southwest Fisheries Center, NMFS, NOAA. In addition to the seasonal trend, short-term episodes of seaward and shoreward transport produce day-to-day, even hour-to-hour, changes in the foods available to

TABLE 5.—*Continued.*

Rank	Food organism: Taxa (rank index)	In diet: Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	In plankton: Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
8	CTENOPHORA (4.73)	**11–20**	**10**	**0.43**	**1.1**	—	**0**	**0.00**	**0.0**
	Plerobrachia bachei	11	5	0.09	0.1	—	0	0.00	0.0
	Others	20	5	0.34	1.0	—	0	0.00	0.0
9	MYSIDACEA (4.47)	**6–20**	**14**	**0.29**	**1.2**	**3–8**	**50**	**1.80**	**0.5**
	Acanthomysis sculpta	6	5	0.19	1.0	—	0	0.00	0.0
	Others	18–20	10	0.10	0.2	3–8	50	1.80	0.5
10	CALANOIDA (1.18)	**2–5**	**14**	**0.28**	**0.3**	**1–5**	**100**	**684.00**	**25.6**
	Nauplii	—	0	0.00	0.0	—	0	0.00	0.0
	Acartia spp.	—	0	0.00	0.0	<1–1	25	229.50	7.5
	Calanus pacificus	2–3	14	0.14	0.1	1–3	100	110.70	3.8
	Eucalanus californicus	5	10	0.14	0.2	3–5	50	12.60	0.8
	Rhincalanus nasutus	—	0	0.00	0.0	—	0	0.00	0.0
	Others	—	0	0.00	0.0	1–2	100	331.20	13.5
OTHER CATEGORIES									
	Molluscan larvae	—	0	0.00	0.0	<<1–<1	50	38.70	2.5
	Cyclopoida	—	0	0.00	0.0	1	75	61.20	1.5
	Cirripedean larvae	—	0	0.00	0.0	1–2	75	24.75	0.5
	Reptantian larvae	4	<1	0.05	<0.1	<1–3	100	240.30	9.3
	Larvacea	—	0	0.00	0.0	3–6	50	6.30	1.3
	Chaetognatha	—	0	0.00	0.0	5–35	75	14.85	5.0
	Fishes	8–10	<1	0.10	NR	3–7	75	7.65	2.8
UNIDENTIFIABLE MATERIAL[5]		—	—	—	19.1	—	—	—	—

No. fish examined: 38
200–345, $\bar{x}$ = 265.3 mm SL
No. empty: 17
$\bar{x}$ no. prey: individuals = 45.2
taxa = 4.8

No. plankton collections: 4
$\bar{x}$ no. zooplankters: 634.3

[1]Value is estimated mean number per 100 m³ of water, based on water filtered (54.8 m³) during the 5-min collection.
[2]Adult *S. mystinus* often were seen feeding on large individuals of *Cyanea capillata*, which were avoided by us during plankton collections because they would have made collections unmanageable.
[3]NR = not recorded. The enumeration was either omitted or unfeasible.
[4]*Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[5]Digested beyond recognition.

planktivorous fishes. The following discussion considers how the diet of *S. mystinus*, summarized in Figure 13, is influenced by these alternations in surface transport during distinct upwelling and downwelling seasons.

The Upwelling Season

The spring-summer upwelling season produces optimal feeding conditions for *S. mystinus*. During this period the combined effects of increased nutrients (from strong upwelling) and increased daylight (from longer days, higher sun-angle, and less storm-produced sediments in suspension) result in growth of diatom populations that constitute the food-base of the zooplankton community.

Seaward Ekman transport in response to the season's persistent northerly winds carries the upwelled nutrients and increasing number of diatoms offshore, where the response of zooplankters can be spectacular. Consider, for example, thaliaceans, which are a major prey of adult *S. mystinus*. Recent study has shown that populations of *Salpa fusiformis* (a common thaliacean in the California Current) normally are food-limited, but can grow rapidly when diatoms are abundant (Silver 1975). In response to a diatom bloom, *Thalia democratica* (another salp common in the California Current), can increase in size by up to 10%/hour and in numbers up to 2.5 times/day, the highest rate recorded for a metazoan animal (Heron 1972a, b).

Zooplankters thus increased in size and number are then carried to *S. mystinus* near shore by the shoreward flow that develops with relaxation of upwelling, or, more forcefully, with shoreward Ekman transport under southerly winds. It remains uncertain, however, whether the numbers of zooplankters entering the Mendocino nearshore habitats are in fact related to the productivity of local upwelling. Wickett (1967) concluded that zooplankton abun-

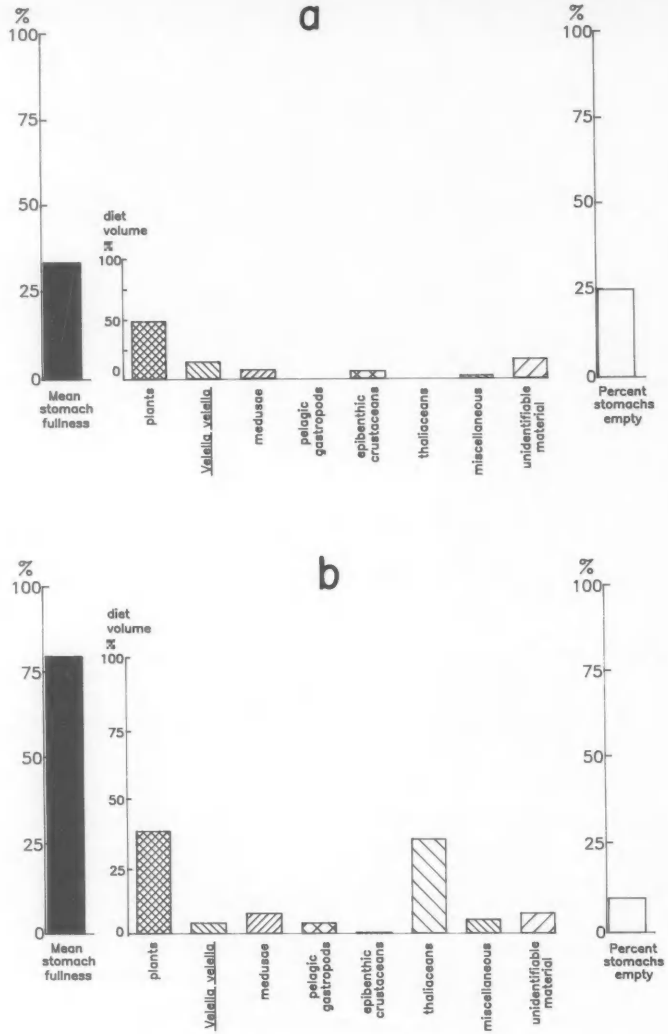

FIGURE 13.—Seasonal variations in the diet of *Sebastes mystinus*:
a. Diet during upwelling episodes of the upwelling season. $n = 51$.
b. Diet during downwelling episodes of the upwelling season. $n = 85$.

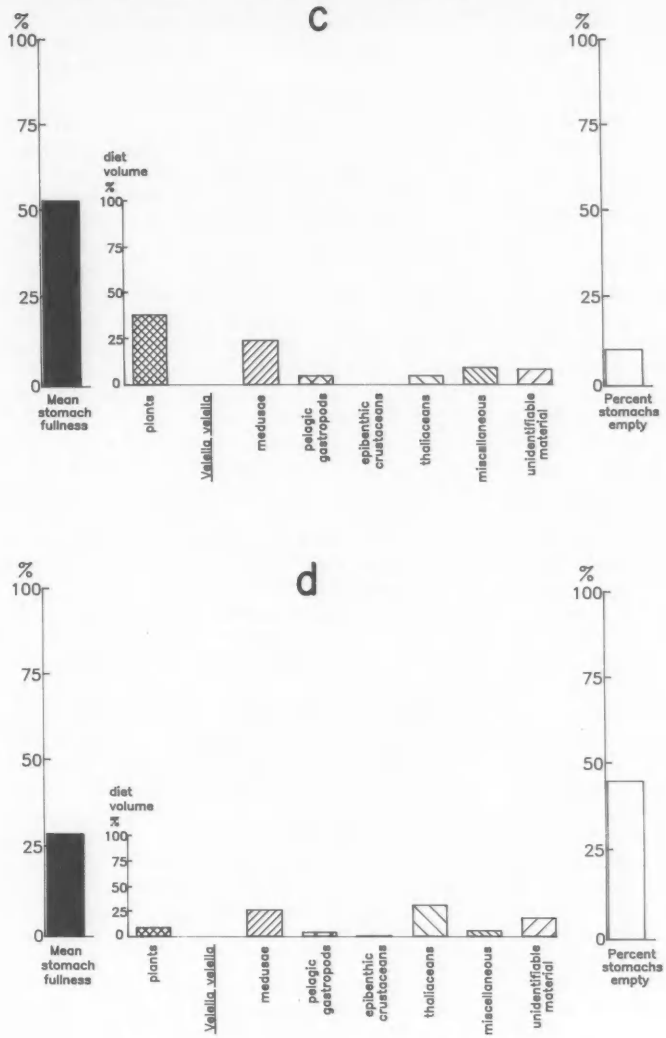

FIGURE 13.—*Continued*—Seasonal variations in the diet of *Sebastes mystinus*:

c. Diet during fall of the downwelling season. $n = 73$.

d. Diet during winter of the downwelling season. $n = 38$.

dances off California depend on nutrients from the Gulf of Alaska, and Chelton et al. (1982) concluded not only that phytoplankton off California depend on nutrients from higher latitudes but also that wind-forced coastal upwelling is relatively unimportant in supplying these nutrients. Despite this uncertainty, growth in thaliaceans is so rapid that it would seem at least many of those off the Mendocino coast could result from local upwelling. Regardless of what determines the growth of thaliaceans in this region, their appearance in large numbers next to the beach is evidence that shoreward transport has developed. These animals are readily detected by in situ observations, and also by their occurrences in samples of both plankton and gut contents (Table 3).

Intermittent shoreward transport during the upwelling season seems especially strong off northern California. This is evident in the upwelling indices of Bakun (1973), and also in that fewer thaliaceans get inshore at this time of year, both to the north, off Oregon (Hubbard and Pearcy 1971), and to the south, off central and southern California (Blackburn 1975). Thus, it is clear that the major foods of *S. mystinus* along the Mendocino coast are most available during downwelling episodes of the upwelling season.

Despite the increased productivity of the upwelling season, *S. mystinus* experiences relatively poor feeding conditions during that season's upwelling episodes. Not only are fewer prey taken during upwelling than during downwelling, a higher proportion of the fish have empty stomachs (Fig. 13). This is because the shoreward flow that transports zooplankters from offshore during downwelling is replaced by the seaward flow that is part of the upwelling condition.

There is, however, one relatively large gelatinous zooplankter from offshore that is most available as prey during upwelling. This is the chondrophore *Velella velella*, a pelagic hydrozoan known as "by-the-wind-sailor". It is, in fact, entirely because of this animal that the food category "Pelagic Hydrozoa" ranked second as food during upwelling episodes (Table 2). Because *V. velella* floats on the water's surface and is equipped with a sail-like structure (Fig. 8), its movements are determined more by wind than by current. The species includes two forms distinguished by whether their sails are oriented to the left of or to the right of the main body axis. This orientation determines their direction in sailing before the wind—left-handed individuals sail to the left of the wind direction and right-handed individuals sail to the right (Bieri 1959). Although it has been reported that the right-handed form predominates off California (Morris et al. 1980), all those we examined from off Mendocino were left-handed, and so would have been driven shoreward by the northerly winds that generated upwelling.

In the absence of favored open-water zooplankters, *S. mystinus* increased consumption of nearshore hyperbenthic zooplankton, e.g., mysidaceans and gammarideans (Table 2). But fewer of these organisms were taken than might be expected, based on their great abundance during much of the upwelling season. *Acanthomysis sculpta*, the mysid most often taken as prey, typically aggregates in large swarms within 2 m of the seafloor. To prey on them, adult *S. mystinus* must leave the upper levels of the water column in a departure from their usual feeding mode that may reduce feeding effectiveness. In addition, most hyperbenthic zooplankters probably are too small to be ready prey of these fish. Although 5–7 mm mysids (Table 2) should be large enough, most other taxa are less than 2 mm. Organisms as small as 1 mm occur in the diet, including some thought to be strictly benthonic, e.g., smaller of the gammaridean *Jassa* sp. (which also occurred in plankton collections; Table 2). But such forms may be ingested (and taken by plankton nets) while attached to drifting plant fragments. Although *S. mystinus* has a smaller mouth than most of its congeners, presumably as an adaptation to planktivory (Hallacher and Roberts 1985), the adults appear unable to consume the larvae of neritic species, e.g., cirripedeans, that, with maximum dimensions of 1 mm or less, often are the most numerous of the zooplankton (Table 2). These larvae are major prey of juvenile *S. mystinus* (unpubl. data; Gaines and Roughgarden 1987), which further suggests it is their small size that precludes them as prey of the adult.

Foods most often consumed in the absence of preferred zooplankters, however, were plant materials. In fact, during upwelling episodes more plants were consumed than anything else (Table 2), and even during downwelling plants were the second-ranked food category (Table 3). Although these rankings are inflated by undigested plant tissues, certain algal materials appear to be important foods. The availability of plant foods to supplement prey shortages was strongly seasonal, however. Thus, the sharply reduced availability of plants during winter and early spring undoubtedly contributed to the prevalence of empty stomachs among fish collected at those times.

Although a wide variety of plants were ingested, *S. mystinus* seemed able to utilize only certain algal tissues. These included zoospores of *Nereocystis leutkeana* and the two epiphytes, *Porphyra nereocystis* and *Smithora naidum*. Probably this is because as members of a carnivorous family they have only limited abilities to digest plant material.

The zoospores of *N. leutkeana* are especially vulnerable to *S. mystinus* when the sori have dropped from the plants' fronds, because at this time the sori have lost their epidermis (an adaptation of the mature sori that facilitates release of the zoospores (David C. Walker[2]). Zoospores may be appropriate food for this largely carnivorous fish because they are, as their name implies, animal-like: they have cell membranes but not the cellulosic cell walls (Wilson 1952) that preclude plants as food for many fishes (e.g., Lobel 1981). The other algae apparently utilized—*Porphyra nereocystis* and *Smithora naidum*—may be appropriate forage for a fish with limited herbivorous abilities because they are monostromatic plants only 25–60 μ thick (Abbott and Hollenberg 1976). So while Gotshall et al. (1965) reported that algae in the guts of *S. mystinus* generally are undigested, some forms appear to be important foods.

It is possible that plant materials are among items of little or no food value that are ingested during food shortages simply because at such times the adult *S. mystinus* become less discriminating in their choice of drifting objects. On the other hand, it is also possible that these fish have unusual herbivorous abilities as a result of adaptations to a diet rich in thaliaceans, which are among the few animals with cellulosic tissues (Berrill 1961). This second possibility is weakened, however, by the fact that the cellulosic tunics of the thaliaceans appear to pass through the gut undigested (Gotshall et al. 1965; our observations).

The Downwelling Season

As the downwelling season developed in the fall, *S. mystinus* experienced progressively poorer feeding conditions. Offshore water flowing into the nearshore habitats at these times tended to be poor in phytoplankton (hence its transparency and blueness, in contrast to the turbid greenness of a few months before), and so generally lacked the herbivorous thaliaceans that were major prey during periods of peak feeding. Relatively large gelatinous zooplankters continued on occasion to be numerous in the shoreward flow, but the species at this time tended to be carnivores rather than herbivores, and *S. mystinus* did not feed on some of them. For example, while siphonophores made "Pelagic Hydrozoa" the top-ranked food category (Table 4), the most numerous pelagic hydrozoan in the water column, *Eutonina indicans*, went virtually untaken. (The small medusae visible throughout Figure 1, especially against the dark kelp, are of this species.) On the other hand, another relatively large, gelatinous zooplankter, the ctenophore *Pleurobrachia bachei* (Fig. 10), was prominent both as prey and in the plankton. Probably the presence of *P. bachei* accounted for the gut-content occurrences of the hyperiid *Hyperoche medusarum*, which is a parasite of this ctenophore (Brusca 1970).

As was true during late spring and summer, certain plant materials became major foods during the fall when favored zooplankters were in short supply. But unlike late spring and summer, when many different plant forms were taken, virtually the only plant materials consumed in the fall were the sori of *N. leutkeana*. This reflected a decreasing abundance of other plants in the environment at the time. Nevertheless, while sporophytes of *N. leutkeana* were fewer in fall than in summer, those present were larger, more mature, and produced more sori.

Although winter produced the poorest feeding conditions of the year, with by far the highest incidence of empty stomachs among the fish examined (Figure 13; also noted by Gotshall et al. 1965), occasionally the waters flowing into the nearshore habitats were rich in offshore zooplankters, including thaliaceans, and at these times the fish fed well. Our sampling of the highly varied winter conditions was not frequent enough to recognize a pattern, but they differed from fall conditions. In general, the distinctive fall and winter conditions off Mendocino matched the "oceanic" and "Davidson Current" oceanographic seasons defined by Skogsberg (1936) and Bolin and Abbott (1962) for Monterey Bay.

Ekman Transport and the Distribution of *Sebastes mystinus*

Ekman transport may be important to the distribution of *S. mystinus*. This is implicit in our finding that alternations between seaward and shoreward surface transport produce feeding opportunities for

[2]David C. Walker, Department of Botany, University of British Columbia, Vancouver, British Columbia V6T 1W5, Canada, pers. commun. 10 May 1977.

which the species is particularly well adapted. Along the west coast of North America, these alternations are best developed off northern and central California (Bakun 1973; Bakun et al. 1974; Mason and Bakun 1985). And not only is *S. mystinus* most numerous off this same section of the coast, it is perhaps the dominant fish in the nearshore habitat there (Hallacher and Roberts 1985; Bodkin 1984; our observations). Although the species is reported from northern Baja California, Mexico, to the Bering Sea (Miller and Lea 1972), its numbers are sharply reduced northward from northern California (Alverson et al. 1964; Frey 1971; Hart 1973) and southward from central California (Hubbs 1948; Limbaugh 1955; Quast 1968). Although undoubtedly other factors are involved, we suggest that occurrences of *S. mystinus* in these northern and southern regions are limited by less favorable feeding conditions.

ACKNOWLEDGMENTS

Daniel Howard assisted in the field work and performed various aspects of data processing. Michael Bowers prepared the histological sections represented by Figure 7, and Louis Rouleau, NOAA weather observer at Mendocino, provided wind data used in Figures 4 and 9. For constructive criticism of the manuscript we thank Andrew Bakun, John Hunter, William Pearcy, and Richard Rosenblatt. Rahel Fischer typed the manuscript.

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Lg 744

THE REPRODUCTIVE BIOLOGY OF TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS* GOODE AND BEAN, FROM THE UNITED STATES MID-ATLANTIC BIGHT, AND THE EFFECTS OF FISHING ON THE BREEDING SYSTEM

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ABSTRACT

To investigate the reproductive biology of tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, we sampled the commercial longline fishery from 1978 to 1982. Results suggested that tilefish are fractional spawners from March to November with a spawning peak from May to September. Estimates of fecundity ranged from about 195×10^3 to 10×10^6 (for 53 cm FL, 2.1 kg and 91 cm FL, 13 kg females), but only 60–85% of the ovarian eggs appeared to have been released by the end of the spawning season.

Tilefish are apparently gonochoristic however, some adult males had slight amounts of ovarian tissue within the testicular mass. Sex ratios were skewed in favor of males at larger sizes; however, both sexes were present at most ages. All juveniles and unsexed fish (<400 mm FL) appeared to be female (i.e., gonad cell structure consisted of oogonia and previtellogenic oocytes), suggesting that some tilefish may undergo prematurational sex reversal, or that early gonad development involves an all female appearing stage.

Tilefish may have a complex breeding system that is behaviorally mediated. Both sexes are functionally mature at ca. 50 cm FL and 5 years, but some males appear to delay participation in spawning for 2–3 years and 10–15 cm in additional length. Tilefish are sexually dimorphic, with males attaining larger sizes and developing conspicuously enlarged predordal adipose flaps (an apparent indicator of male breeding status) at 65–70 cm FL (6–7 years), when males begin to participate in spawning (i.e., develop large testes), not when they are functionally mature (i.e., producing sperm).

The rapidly expanding fishery from 1978 to 1982, which reduced population density by one-half to two-thirds, may have altered the breeding system by causing males to spawn at smaller sizes (10 cm) and younger ages (2–2.5 years) in 1982 than in 1978.

Tilefish, *Lopholatilus chamaeleonticeps* (Branchiostegidae), is a demersal gonochoristic species found along the outer continental shelf from Nova Scotia south to Surinam (Dooley 1978; Markle et al. 1980). Within the Mid-Atlantic Bight (continental shelf between Cape Cod, MA and Cape Hatteras, NC), they inhabit a narrow zone of relatively warm temperatures (9°–14°C) in about 80–240 m depths. Following a brief period as pelagic larvae (Fahay and Berrien 1981; Berrien 1982), juveniles settle to the bottom. Adults are sexually dimorphic, males having larger adipose flaps (= predorsal crest of Dooley 1978) than females (Katz et al. 1983). Growth in both sexes is about 10 cm per year for the first four years, then it slows, but more so in females than males (Turner et al. 1983). Maximum size of females is about 100 cm FL and 112 cm FL in males, and maximum ages are 35 and 26 years, respectively (Turner et al. 1983).

Both juveniles and adults select sedimentary substrata, and seek shelter in a variety of habitats. Grossman et al. (1985) found a strong correlation between sediment composition and tilefish occurrence. Juveniles and adults occupy highly contageously distributed vertical burrows, the primary habitat, in Pleistocene clay substrata (Able et al. 1982; Grimes et al. 1986). Adults also inhabit horizontal excavations in more vertically oriented clay sediments of submarine canyon walls called "pueblo habitats" (Cooper and Uzmann 1977; Warme et al. 1977; Grimes et al. 1986), and scour depressions under and around glacial erratic boulders (Valen-

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Manuscript accepted April 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

tine et al. 1980; Grimes et al. 1986). Several crustaceans and fishes are concentrated in and near tilefish excavations, which are formed by the combined activity of tilefish and their associates (Able et al. 1982; Grimes et al. 1986). Several associates are important components of tilefish diets, suggesting close trophic linkages within the burrow community (Turner and Freeman MS[5]; Grimes et al. 1986). Limited mark-recapture data suggests that tilefish are sedentary (Grimes et al. 1983). Tilefish and their associates have definite temporal activity patterns, and male-female pairing may occur (Grimes et al. 1986). Habitat preference, contagious distribution within suitable clay substratum, definitive activity patterns, limited movement, and pair bonding provide opportunities for social interaction and organization within populations.

Commercial landings of the Mid-Atlantic–southern New England tilefish stock (Katz et al. 1983) have varied widely since 1916 when 4,500 metric tons (t) were landed in 10 months (Freeman and Turner 1977). In the early 1970s an important longline fishery developed, centered in New York-New Jersey, and landings increased. This fishery became one of the most valuable finfisheries in both states during most years since 1978 (Grimes et al. 1980; U.S. Department of Commerce 1980a–c; D. J. Christensen pers. commun.[6]). From 1977 to 1980, annual landings were 2,061, 3,412, 3,840, and 3,575 t, but catches declined to 3,200 and 1,900 t in 1981 and 1982 (U.S. Department of Commerce 1980a–c; D. J. Christensen fn. 6). Effects of fishing on the stock have been drastic, reducing stock size by one-half to two-thirds from 1978 to 1982 (Turner 1986).

The purpose of this paper is to describe the reproductive biology of tilefish in the northern stock, and present evidence that participation in spawning by males is socially mediated. Furthermore, we show that the mating system has been modified by commercial fishing.

MATERIALS AND METHODS

Samples of tilefish from the United States Mid-Atlantic–southern New England area were obtained from domestic longline and New Jersey recreational (headboat[7]) fisheries. Information gathered for each sample included the statistical nature of the sample (random or nonrandom), capture method, location (LORAN C), date, and length (FL, cm), sex, weight (whole and eviscerated), and height (mm) of the adipose flap of each animal. When possible, gonads were excised, weighed (0.1 g) and preserved in 10% formalin. We assigned each fish to one of three classifications (male, female, or unknown) and one of six stages of sexual maturity following visual examination (Nikolsky 1963). Some fish used for reproductive studies were aged using thin sections of their saggital otoliths (Turner et al. 1983).

Routine histological sectioning and staining (haemotoxylin and eosin) techniques and light microscropy (450× and 1000×) were used to examine gonad structure of six small fish (<50 cm), and assess the state of sexual maturity. Ovarian development corresponded to that described by Moe (1969) for red grouper, *Epinephelus morio*, and Yamamoto (1956) for the flounder *Liopsetta obscura*. Spermatogenic development was identical to that of *Tilapia leucosticta* (Hyder 1969) and toadfish, *Opsanus tau*, (Hoffman 1963). Females were assessed as immature when ovaries contained only previtellogenic and early vitellogenic oocytes (Yamamoto 1956; Moe 1969; Waltz et al. 1982; Ross 1978; Erickson and Grossman 1986). Males were considered mature when active spermatogenesis was occurring and spermatozoa were present in spermatogenic tubules (Ross 1978). Limited spermatogenesis occurred in the testes of some immature males (Erickson and Grossman 1986).

A gonosomatic index (GSI) was calculated for females according to the formula $GSI = \frac{GW}{BW} \times 100$, where GW = fresh gonad weight (g) and BW = fresh eviscerated body weight (g) (Nikolsky 1963), for describing spawning seasonality. The seasonal progression of mean ovum diameters was also used to establish the reproductive seasonality, and the ovum-diameter frequency distribution for ripe females was used to indicate spawning frequency (isochronal vs. heterochronal) (Hickling and Rutenberg 1936). Separated ova from each fish were placed in liquid and stirred; a random sample for measuring was then obtained by extracting three aliquots with a large syringe. Diameters of 500–1,000 ova from each female were measured (nearest ocular micrometer unit) using a binocular dissecting scope and a filar micrometer. We assumed

[5]Turner, S. C., and B. L. Freeman. Food habits of tilefish, *Lopholatilus chamaeleonticeps*. Unpubl. manuscr. Southeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Miami, FL 07732.

[6]D. J. Christensen, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732, pers. commun. 1983.

[7]Headboats are vessels which charge anglers for fishing on an individual, thus "per head", basis.

uniform ova size (developmental stage) distribution among anterior to posterior ovarian lobe locations, as has been demonstrated for *Lopholatilus chamaeleonticeps* from the South Atlantic Bight (Erickson et al. 1985).

To determine if the liver was being utilized to store energy in the form of fat reserves to be used in gonad maturation, we calculated a hepatosomatic index (HSI) = liver weight (g)/gutted body weight (g) × 100 (Htun-Han 1978).

Ovaries used to estimate fecundity (= ovarian egg count of Gale and Deutsch (1985)) were preserved in modified Gilson's fixative (Bagenal and Braum 1978). The ovarian tunic was removed and washed free of adhering ova. Developing ova were separated from folicular material and most oogonia by washings under a stream of water. Based upon initiation of yolk accumulation, all oocytes with diameters >0.15 mm were included in ovarian egg counts. Each sample of developing ova was diluted in water and stirred, then at least two subsamples pipetted; each subsample was placed in a 6 × 6 cm gridded Petri dish for counting. Ova were counted in six randomly selected grid squares, and the average number of ova in the six squares was then adjusted to the total subsample count by multiplying the average by the total number of grid squares in the dish. The sample and subsamples were oven dried at 40°C for at least 24 hours and weighed to the nearest 0.001 g on a Mettler[6] balance. Fecundity (total ovarian egg count) was estimated as the number in the subsample multiplied by sample weight divided by subsample weight.

Predictive equations of fecundity from length and weight were fit using least squares regression and converted to functional regressions (Ricker 1973). Fecundity was separately regressed on FL and gutted weight using all possible combinations of untransformed log and semi-log models. We inspected residuals, plots and coefficients of determination to evaluate fits.

RESULTS

Gonad Structure and Sex Determination

Males smaller than 600 mm FL were difficult to sex by gross gonadal structure because testes were small and undeveloped. However, in females larger than about 400 mm FL ovaries were sufficiently developed to visually determine sex easily. Therefore, we histologically examined gonadal tissues of 155 fish (50 males, 545–814 mm FL; 52 females, 241–678 mm FL; and 53 juveniles, 146–400 mm FL). Based upon gonad microstructure, seven fish between 467 and 592 mm FL that were macroscopically unsexable were males. All juveniles and unsexed fish <400 mm FL (79 fish 121–400 mm FL) appeared to be females, i.e., had cell structure consisting of only oogonia. These cells had slightly acidophilic cytoplasm and distinct, but irregular, cell membranes. The nuclear membrane was less obvious because it was masked by basophylic nuclear material located peripherally.

The paired ovaries of adult *L. chamaeleonticeps* are suspended below the swimbladder from the dorsal body wall in the extreme posterior of the body cavity. Ovarian microstructure and development are identical to *Caulolatilus microps* (Ross and Merriner 1983) and *L. chamaeleonticeps* (Erickson et al. 1985) from the South Atlantic Bight and are described in detail by Idelberger (1985).

The testes of tilefish are solid, smooth textured, and more elongate than ovaries. In males smaller than about 65 cm FL, testes were not obviously lobed and were pinkish in color. Only in large adult males were testes creamy white and heavily lobed. Microstructure of the testes was typical of teleosts (Hoffman 1963; Smith 1965; Hyder 1969) and was identical to *C. microps* (Ross and Merriner 1983), and, like the ovary structure, was described in detail by Idelberger (1985). Two males (604 and 609 mm FL) had slight amounts of ovarian tissue within the testicular mass (Fig. 1). That ovarian tissue consisted of several resting or previtellogenic (perinucleolar) oocytes located in testicular mass with definite spermatogenic tubules and crypt structure.

Sexual Dimorphism

The predorsal adipose flap is sexually dimorphic in adult tilefish and can easily be used to determine sex in animals larger than about 70 cm FL. The size of the predorsal flap was significantly larger in males than in females older than age 5 years and larger than 65 cm FL (Table 1). It was not possible to compare predorsal flap sizes of the largest males to those of females, because females do not grow as large as males (Turner et al. 1983; Harris and Grossman 1985).

Sexual Maturity

We determined the general pattern of age and size of sexual maturity using both visual staging and

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

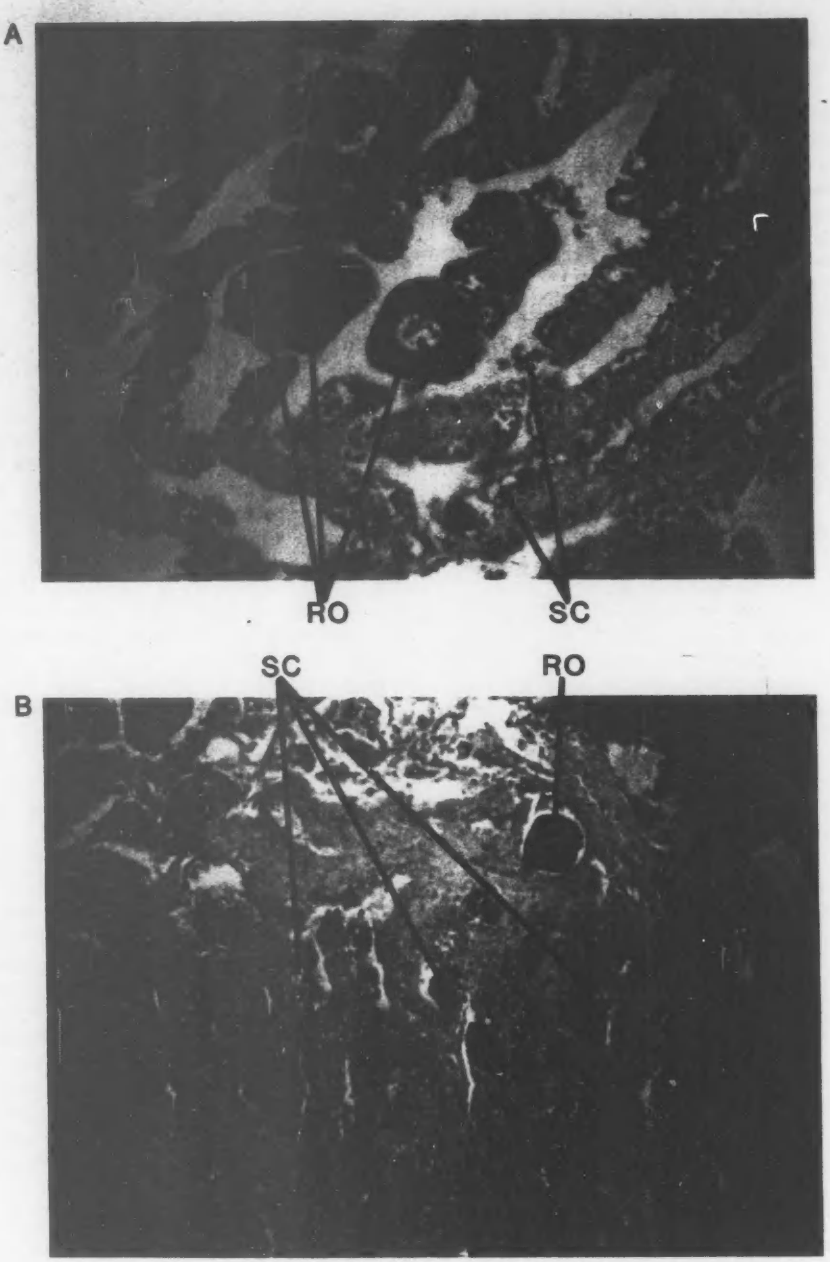

FIGURE 1.—Photomicrographs of histological sections of tilefish testes from a 60.4 cm FL male at ×400 (A) and a 60.9 cm FL male at ×100 (B) showing residual oocytes (RO) and spermatogenic cripts (SC).

TABLE 1.—Mean ($\bar{X}$) and sample size (N) for predorsal adiposal flap height at size and age for male and female tilefish, and students t-tests of flap height differences between sexes.

	Males		Females			
	$\bar{X}$ (mm)	N	$\bar{X}$ (mm)	N	t-value	Probability
Size (FL, mm)						
45–49	20.1	13	17.1	19	1.02	N.S.
50–54	23.1	29	23.6	49	0.33	N.S.
55–59	25.7	36	25.9	62	0.04	N.S.
60–64	30.6	40	27.6	105	0.91	N.S.
65–69	37.1	73	31.6	101	2.63	<0.01
70–74	49.8	67	31.7	51	3.58	<0.01
75–79	61.8	30	37.6	25	4.05	<0.01
80–84	72.3	30	37.7	11	1.90	<0.05
85–89	82.4	12	28.8	8	1.84	<0.05
90–94	68.0	1	38.5	2	Not testable	
95–99	63.0	1	—	0	Not testable	
100–104	98.0	8	—	0	Not testable	
Age (years)						
3	—	0	5.0	6	Not testable	
4	—	0	8.1	7	Not testable	
5	20.5	6	20.4	16	0.018	N.S.
6	36.2	23	21.6	32	6.63	<0.001
7	33.2	41	27.9	51	3.42	<0.01
8	44.0	40	30.1	42	5.64	<0.001
9	51.4	17	30.4	40	5.97	<0.001
10	57.4	8	32.9	35	5.45	<0.001
11	65.0	4	31.9	16	5.59	<0.001
12	—	0	30.9	9	Not testable	
14	—	0	36.5	2	Not testable	
15	112	1	36.8	14	Not testable	

histological data pooled over all years of the study. The two methods gave substantially different results for males; however, both visual and histological data suggested that all females matured at 60–65 cm FL and 8–9 years of age (Figs. 2, 3). Visual staging indicated that virtually all males were mature at 80–85 cm FL and 10–11 years. In contrast, histological results indicated almost all males were mature at 65–70 cm FL (estimated age 7–8 years, Turner et al. 1983) (Figs. 2, 3). That is, visual staging suggested that females matured about 20 cm smaller and 2–3 years younger than males; however, according to histological analysis, both males and females were mature and producing gametes at a similar size (60–70 cm FL). Thus, these results show that although males were producing sperm at 65–70 cm FL (estimated 7–8 years, Turner et al. 1983), they were not developing a large testicular mass until 80–85 cm FL and age 10–11 years.

We reasoned that predorsal adipose flap size might be a sign of maturity or reproductive status of males, because the height of the flap was larger in males than females above 65 cm and age 5 years (see previous section on Sexual Dimorphism). Additionally, the development of enlarged adipose flaps in males coincided with the size of 50% maturity (60–65 cm FL) as judged by development of enlarged testes (i.e., visual method), not at the smaller size of 50% maturity (50–55 cm FL) determined histologically (Fig. 2). Therefore, if predorsal adipose flap height were a sign of reproductive status in males, then mature males should have larger flaps than immature males; and this was so (Fig. 4). Furthermore, ANCOVA (with FL as the covariate) indicated that flap height was significantly larger in mature males than immature males (Table 2).

TABLE 2.—Mean and ANCOVA (with FL as the covariate) of predorsal adipose flap height in sexually mature and immature male tilefish. Flap height data set tested was restricted to a size range containing both mature and immature males (50–75 cm FL). df = degrees of freedom, ss = sum of squares, N = sample size, and $\bar{X}$ = mean.

	MEAN		
	N	$\bar{X}$ flap height (mm)	X FL (cm)
Immature	94	28.7	59.4
Mature	87	42.7	68.6

	ANCOVA			
Source	df	ss	F	$P > F$
Maturity	1	504.4	6.42	0.0121
FL	1	7,423.4	94.56	0.0001
FL X maturity	1	605.1	7.71	0.0061
Error	177	13,895.7		
Total	180	30,365.8		

Because we had studied reproduction during a period of rapid expansion of the fishery, i.e., the commercial longline fishery had decreased the tilefish population by one-half to two-thirds from 1978 to 1982 (Turner 1986), we decided to examine the data to determine if the fishery had affected the size at which tilefish were developing enlarged testes (i.e., attaining maturity as assessed by the visual method). A comparison of visually assessed sexual maturity at size and age for 1978 and 1982 suggested that females <50 cm FL were maturing at a smaller size in 1978 than in 1982, but that females >50 cm FL matured at very slightly larger sizes in 1978 than in 1982 (Table 3). Log-likelihood contingency tests of these data for females indicated that maturity-at-length was significantly different in 1978 and 1982, but the difference was due to the numbers of mature and immature fish between 41 and 55 cm (Table 3). The data for males <75 cm FL indicated that males matured at smaller size in 1982 than in 1978 (Table 4). A log-likelihood contingency

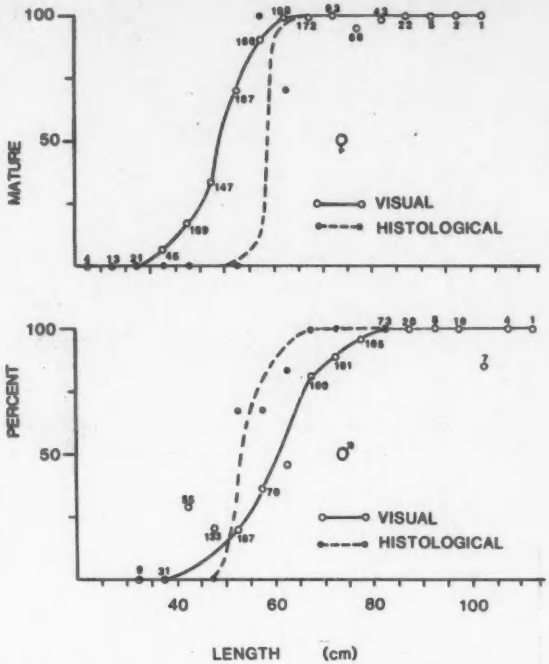

FIGURE 2.—The relationship of sexual maturity (by both visual staging and histological methods) and size (5 cm FL intervals) for female and male tilefish. Sample size is shown next to each point. Curves are fitted by eye.

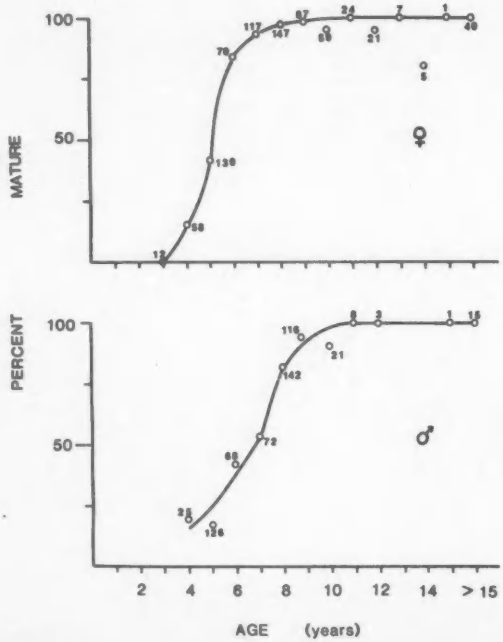

FIGURE 3.—The relationship of sexual maturity (by visual staging) and age for female and male tilefish. Sample size is shown next to each point. Curves are fitted by eye.

TABLE 3.—Female sexual maturity at length (visually determined) and log-likelihood contingency test that maturity at fork length (FL) in female tilefish was not different for 1978 and 1982. Critical chi-square values are $\chi^2_{0.05}$ (11 df) = 19.7 and $\chi^2_{0.01}$ (11 df) = 24.7. NT = not testable.

FL (cm)	1978 Maturity No.	1978 Maturity %	1978 Sample size	1982 Maturity No.	1982 Maturity %	1982 Sample size	G-statistic
26–30	No data			0	0	1	NT
31–35	0	0	7	0	0	3	0
36–40	3	21	14	0	0	17	0
41–45	11	49	23	4	7	60	30.4
46–50	34	81	42	11	15	72	89.6
51–55	54	59	92	41	89	46	56.5
56–60	40	80	50	35	100	35	0
61–65	63	98	64	49	100	49	0
66–70	57	100	57	27	100	27	0
71–75	12	100	12	29	100	29	0
76–80	12	92	13	14	93	15	0.2
81–85	10	100	10	4	100	4	0
86–90	6	100	6	No data			NT
91–95	3	100	3	1	100	1	0
96–100	No data			1	100	1	NT
Total			393			360	176.7

TABLE 4.—Male sexual maturity at length (visually determined) and log-likelihood contingency tests that maturity at fork length (FL) in male tilefish was not different for 1978 and 1982. Critical chi-square values are $\chi^2_{0.05}$ (10 df) = 18.31 and $\chi^2_{0.01}$ (10 df) = 23.2. NT = not testable.

FL (cm)	1978 Maturity No.	1978 Maturity %	1978 Sample size	1982 Maturity No.	1982 Maturity %	1982 Sample size	G-statistic
31–35	0	0	4	No data			NT
36–40	0	0	15	No data			NT
41–45	5	28	18	11	52	21	4.4
46–50	10	24	42	50	79	63	59.9
51–55	13	12	105	16	43	37	47.3
56–60	0	0	15	19	73	26	0
61–65	8	44	18	12	71	17	5.2
66–70	15	60	25	16	89	18	13.7
71–75	31	79	39	15	94	16	8.9
76–80	47	96	49	20	91	22	1.8
81–85	28	100	28	14	100	14	0
86–90	10	100	10	5	100	5	0
91–95	3	100	3	2	100	2	0
96–100	8	100	8	No data			NT
101–105	3	100	3	No data			NT
106–110	1	100	1	No data			NT
111–115	1	100	1	No data			NT
Total			384			241	141.2

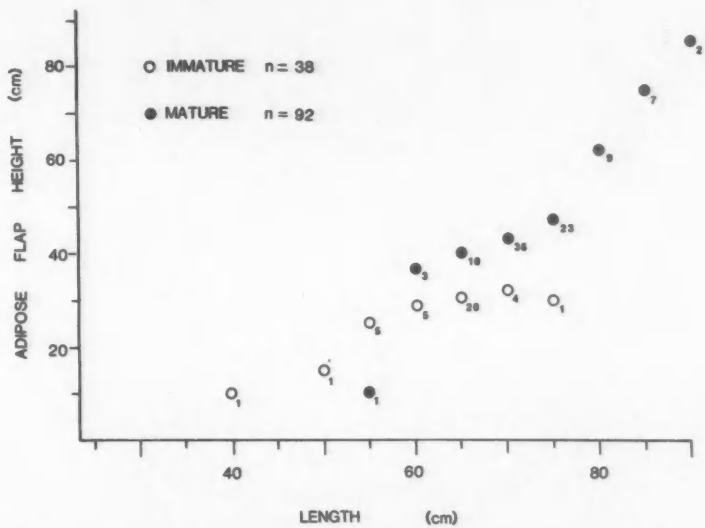

FIGURE 4.—Mean predorsal adipose flap height at length (5 cm FL intervals) for sexually mature and immature male tilefish. Maturity was assessed by visual staging. Sample size is indicated for each interval.

test indicated that maturity-at-age in males for the two years was highly significantly different (Table 4).

Analysis of visual maturity at age data gave less ambiguous results. Percent of females mature at age in 1978 and 1982 was not significantly different (Table 5). However, males matured at younger ages in 1982 than 1978, and the differences between years were highly statistically significant (Table 6).

TABLE 5.—Female sexual maturity at age (visually determined) and log-likelihood contingency tests that maturity at age in female tilefish was not different for 1978 and 1982. Critical chi-square values are $\chi^2_{0.05}$ (9 df) = 16.9 and $\chi^2_{0.01}$ (9 df) = 21.7. NT = not testable.

	1978			1982			
Age (yr)	Maturity No.	Maturity %	Sample size	Maturity No.	Maturity %	Sample size	G-statistic
3	0	0	1	0	0	3	0
4	1	8	13	1	5	19	0.3
5	35	43	82	5	33	15	3.1
6	19	83	23	3	75	4	0.6
7	47	90	52	8	100	8	0
8	68	97	70	20	95	21	0.7
9	14	100	14	14	100	14	0
10	2	100	2	12	100	12	0
11	No data			7	100	7	NT
12	1	100	1	8	100	8	0
13	No data			4	100	4	NT
14	No data			2	100	2	NT
⩾15	9	100	9	4	100	4	0
Total			267			121	4.7

TABLE 6.—Male sexual maturity at age (visually determined) and log-likelihood contingency tests that maturity at age in male tilefish was not different for 1978 and 1982. Critical chi-square values are $\chi^2_{0.05}$ (8 df) = 15.5 and $\chi^2_{0.01}$ (8 df) = 20.1. NT = not testable.

	1978			1982			
Age (yr)	Maturity No.	Maturity %	Sample size	Maturity No.	Maturity %	Sample size	G-statistic
4	1	6	16	3	75	4	34.5
5	10	10	96	7	41	17	44.8
6	3	19	16	8	80	10	27.6
7	6	38	16	6	75	8	22.3
8	41	77	53	15	75	20	0.6
9	23	85	27	19	100	19	0
10	5	100	5	6	86	7	0
11	2	100	2	1	100	1	0
12	1	100	1	2	100	2	0
⩾15	11	100	11	No data			NT
Total			246			88	129.8

TABLE 7.—Sex ratio at length and log-likelihood tests that sex ratio was not different from 1:1 at 5 cm FL intervals. All G scores were calculated using Yates correction for small sample sizes. Critical chi-square values are $\chi^2_{0.05}$ (1 df) = 3.84 and $\chi^2_{0.01}$ (1 df) = 6.64. NT = not testable.

Fork length (cm)	Number of females	Percent	Number of males	G-statistic
46–50	46	46	54	0.6
51–55	95	41	134	6.7
56–60	56	78	16	23.5
61–65	66	78	19	27.5
66–70	74	69	33	16.1
71–75	18	30	43	10.5
76–80	14	21	53	25.8
81–85	13	30	31	7.6
86–90	7	37	12	1.3
91–95	5	63	3	0.4
96–100	0	0	9	NT
101–105	0	0	4	NT
106–110	0	0	2	NT
111–115	0	0	1	NT

Sex Ratio

To minimize the chances of obtaining biased results caused by the effects of fishing we estimated sex ratio at size and age using only data collected in 1978 when the tilefish population was lightly exploited. Proportions of males and females were similar in the 46–50 and 51–55 cm FL intervals, although the ratio in the 51–55 cm FL interval tested significantly different at $P < 0.05$ (Table 7). Males were significantly predominant (70–80%) between 71 and 90 cm FL. At the 91–95 cm FL size females were predominant once again (>50%), although not significantly so (Table 7). Above 100 cm FL only males were collected.

The general pattern of sex ratio at age in 1978 seems to have been equal proportions of the sexes through about age 20 years, with only females present from ages 29 to 36 years. Log-likelihood tests of sex ratio at age showed no significant differences from equality except for ages 7 and 8 years; sex ratio at age was not testable for ages 29–36 years because only females were present (Table 8).

Although sex ratio was skewed with age and size, the estimated sex ratio for the entire population was different from 1:1 in 1978 (Table 9). We calculated the population to be 46.2% males, and could not reject the null hypothesis that sex ratio is not different from 1:1 ($\chi^2 = 0.15$, df = 1, $\chi^2_{0.05} = 3.84$) in the population ⩾50 cm FL.

Spawning

Several lines of evidence suggest that tilefish in the Mid-Atlantic–southern New England area are

TABLE 8.—Sex ratio at age and log-likelihood tests that sex ratio at age was not different from 1:1. All *G* scores were calculated using Yates correction for small sample sizes. Critical chi-square values are $\chi^2_{0.05}$ (1 df) = 3.84 and $\chi^2_{0.01}$ (1 df) = 6.64. NT = not testable.

Age (yr)	Number of females	Percent	Number of males	*G*-statistic
4	1	100	0	NT
5	43	46	50	0.7
6	10	67	5	2.5
7	40	78	11	18.8
8	69	62	42	7.1
9	20	49	21	1.0
10	2	29	5	2.4
11	0	0	2	NT
16	2	40	3	0.8
19	2	50	2	Equality
29	1	100	0	NT
30	1	100	0	NT
31	1	100	0	NT
32	2	100	0	NT
33	1	100	0	NT
34	1	100	0	NT
35	1	100	0	NT
36	1	100	0	NT

TABLE 9.—The proportion of male tilefish in the 1976 population ≥50 cm FL, $P = \sum_{i}^{n} L_i M_i$ where *L* and *M* = the proportion of all fish and males, respectively, in the i^{th} 5 cm FL interval, and *n* = the number of size intervals. L_i was determined from the 1978 commercial longline catch of tilefish.

Fork length (cm) *i*	Proportion of all fish *L*	Proportion of males *M*	Proportion of males in population *P*
<50	0.026	0	0
51–55	0.058	0.540	0.032
56–60	0.158	0.253	0.026
61–65	0.073	0.167	0.012
66–70	0.162	0.267	0.044
71–75	0.191	0.646	0.127
76–80	0.110	0.792	0.089
81–85	0.087	0.744	0.066
86–90	0.682	0.611	0.043
91–95	0.021	0.400	0.008
96–100	0.011	0.875	0.010
≥101	0.036	1.000	0.004
			= 0.462

fractional spawners from about March through November, although most of the reproduction evidently occurs from May to September. Some females with free ova in the ovarian lumen (running ripe) were present in March through August and in October and November. From May through August, 89–98% of the females were ripe or running ripe (Fig. 5). Running ripe or ripe males were not as frequently observed as were females in a similar reproductive state. In fact, only very large males (75–80 cm FL) were observed with a large creamy white swollen testicular mass. Ripe males were found in January, March, May through August, October, and November, but the highest proportions (23–46%) were present in May through August (Fig. 5).

GSI data for females indicated a similar seasonal spawning pattern (Fig. 6). Highest GSI values consistently occurred from May through August, when ovaries accounted for 3.5–8.3% of gutted body weight.

Analysis of ovum-diameter data also suggested that spawning occurred mostly from May to September, and indicated that spawning was fractional, i.e., ova were released in batches. Highest monthly mean developing ovum diameters (0.30–0.42 mm) occurred in May through August (Fig. 7). During these months mean ovum diameter was usually >0.35 mm (Fig. 7). During other months, mean ovum diameter was always ≤0.30 mm. The size-frequency distribution of ova from running ripe females was polymodal (Fig. 8), suggesting multiple spawnings by individual females during the reproductive season.

Tilefish may not utilize the liver and soma to store energy as fat for mobilization to the gonads in preparation for spawning as many species are thought to do (Hoar 1957). HSI for both males and females showed a distinct pattern of seasonal variation, but highest values occurred during summer (spawning season) and lowest in winter (Fig. 9). Somatic condition factor (eviscerated weight, g/FL^3) showed no discernable seasonal pattern in males or females.

Fecundity

Because tilefish are fractional spawners, fecundity (ovarian egg count) was estimated from females collected early in the spawning season (i.e., May to early June) to minimize the chance of using a partially spawned ovary and underestimating egg number. Estimates of fecundity ranged from approximately 195,000 for a 53 cm FL (2.1 kg) female to 10 million for a 91 cm FL (13 kg) female, with a mean egg count of 2.28 million (n = 49, SD = 1.02). The 91 cm FL female with 10 million eggs was exceptional; all other estimates were <4.1 million, even for other large females 80 and 86 cm FL. Therefore, we judged that the two largest fish, 91 and 86 cm FL, were outliers and developed predictive equations for egg count without using outlier data.

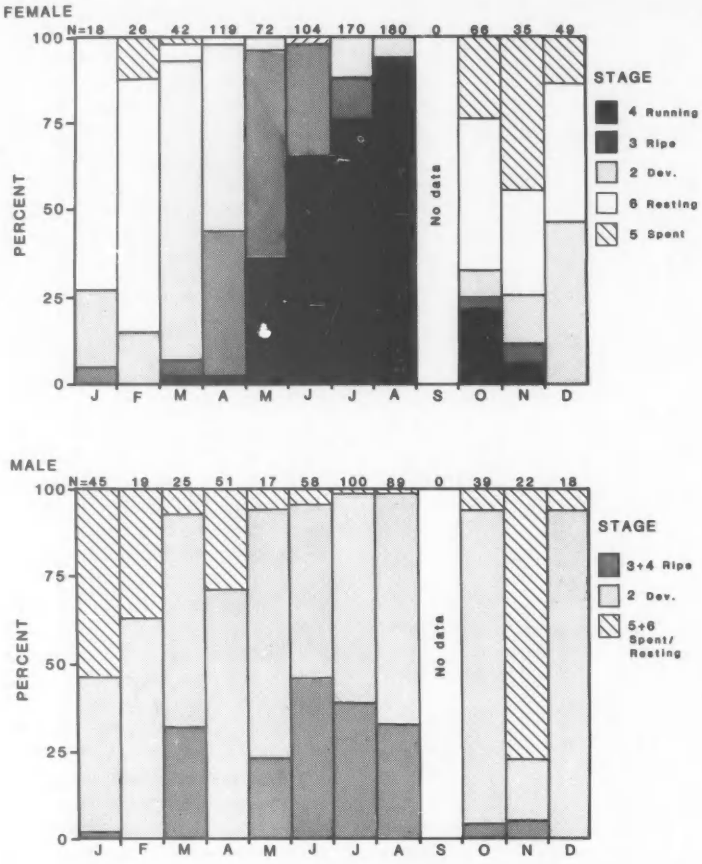

FIGURE 5.—Reproductive seasonality of female and male tilefish as indicated by the percent of various visual maturity stages collected by month from 1978 to 1982.

Log-transformed models produced slightly superior fits, with length proving a slightly better predictor of ovarian egg count than weight ($\log_e Y = 4.75 \log_e FL - 5.2$, $r^2 = 0.62$, $n = 48$; $\log_e Y = 1.48 \log_e W + 2.48$, $r^2 = 0.59$, $n = 48$). Based upon our estimates, a first spawning female would produce <500,000 eggs.

DISCUSSION

Seasonality and Spawning

It seems clear that the northern stock of *Lopholatilus chamaeleonticeps* consists of fractional spawners over an 8 or 9 month season, with peak spawning from May to September. Our findings agree with the limited information previously reported. Collins (1884) reported ripe fish in July; Bigelow and Schroeder (1953) in August; Dooley (1978) in February, March, June, and July; Morse (MS)[9] March through August; and Freeman and Turner (1977) from mid-March to mid-September. Other members of the Branchiostegidae (*Caulolatilus microps*, *C. chrysops*, *C. princeps*, *C. affinis*,

[9]Morse, W. W. Length, weight, spawning and fecundity of the tilefish, *Lopholatilus chamaeleonticeps*, from New Jersey waters. Unpubl. manuscr. Northeast Fish. Cent. Sandy Hook Lab., Natl. Mar. Fish. Serv., NOAA, Highlands, NJ 07732.

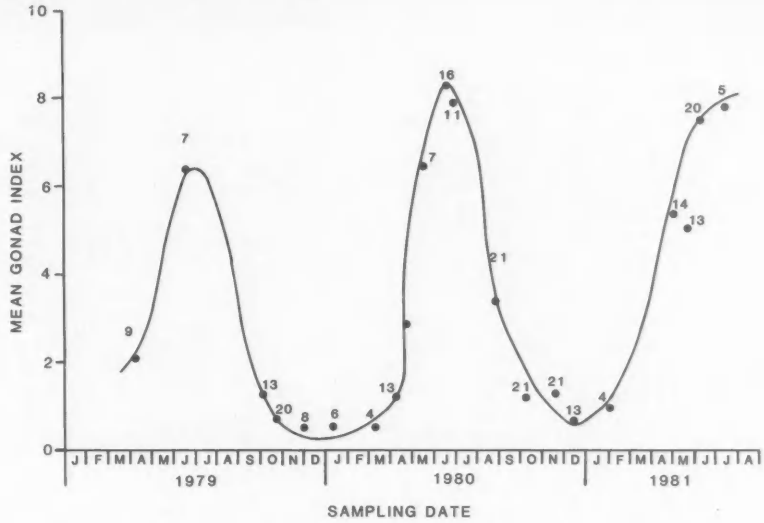

FIGURE 6.—Reproductive seasonality of female tilefish as indicated by monthly mean gonad index. Sample size is indicated for each month.

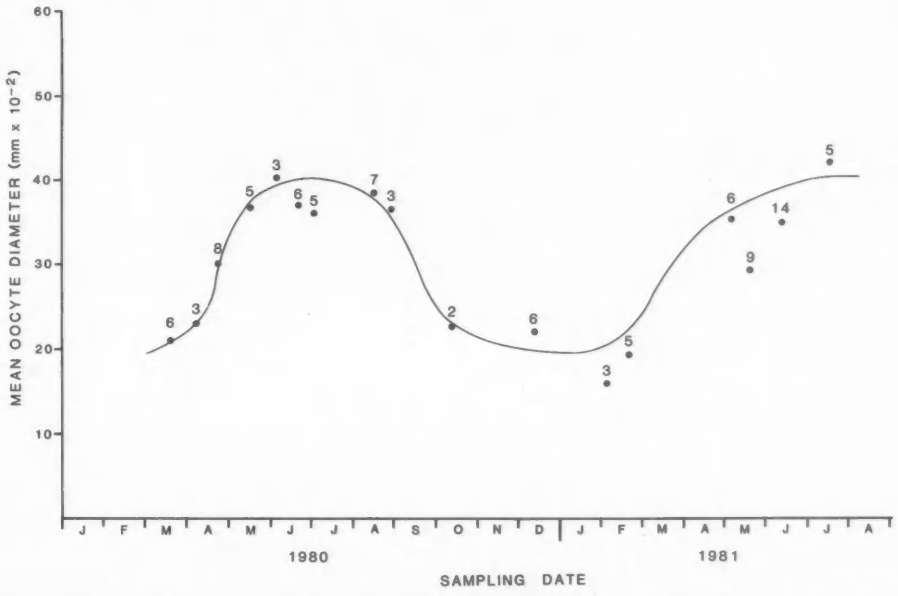

FIGURE 7.—Reproductive seasonality of female tilefish as indicated by monthly mean oocyte diameters. Sample size is indicated for each month.

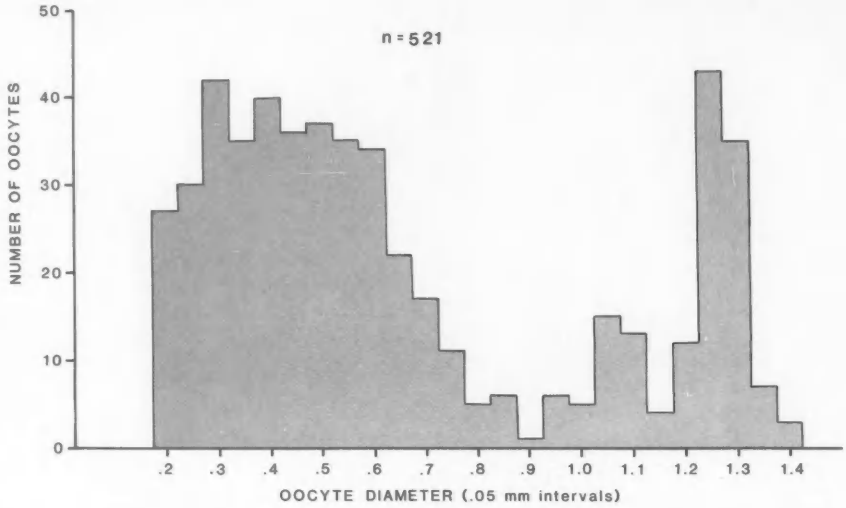

FIGURE 8.—Frequency distribution of oocyte diameters from a spawning 66 cm FL female tilefish (running ripe) collected in June 1979.

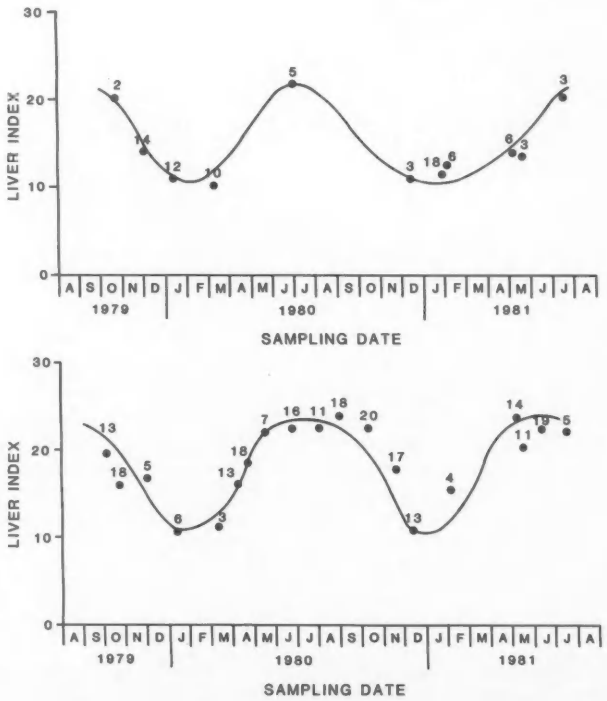

FIGURE 9.—Monthly mean heptosomatic index for male (upper) and female (lower) tilefish. Sample size is shown next to each mean.

Branchiostegus japonicus) all exhibit extended reproductive seasons centered around summer (Hayashi 1977, 1979; Dooley 1978; Ross and Merriner 1983). However, Erickson et al. (1985) reported that *L. chamaeleonticeps* spawned from March through June off Georgia in the South Atlantic Bight. The reason for the shorter reported spawning season for *L. chamaeleonticeps* in the South Atlantic Bight is uncertain.

Fractional spawning by individual females was indicated by the polymodal frequency distribution of ovum diameters. This asynchronous follicular development is typical of fractional spawning (deVlaming 1983), and has been reported for *L. chamaeleonticeps* in the South Atlantic Bight (Erickson et al. 1985) and Mid-Atlantic Bight (Morse fn. 9). Fractional spawning based upon polymodal ovum-diameter distributions has also been reported for the confamilials *C. microps* and *B. wardi* (Dooley 1978; Ross and Merriner 1983).

Our estimates of fecundity in tilefish are consistent with those in the literature. We agree with Gale and Deutsch (1985) that the term fecundity is incorrectly applied to many fishes, especially fractional spawners, because in most cases there is no reasonable means to determine which or how many oocytes or developing ova will be released, or how many ovarian ova will be resorbed after spawning and never released. Therefore, we recognize that our ovarian egg count data provides only a rough estimate of actual fecundity. Erickson and Grossman (1986) found the relationship between fecundity and weight to be best described by a log transformation ($\log_e F = 1.497 \log_e W + 12.59$, $r^2 = 0.93$); while Morse (fn. 9) found the relationship best fitted to a linear form ($F = -966{,}471 + 887\,W$, $r^2 = 0.61$). To compare our estimates further we calculated relative fecundity using extreme point estimates of fecundity reported by other authors (Erickson and Grossman 1986, $414 \cdot g^{-1}$ and $950 \cdot g^{-1}$ for 2.0 and 8.0 kg fish; Morse fn. 9, $543 \cdot g^{-1}$ and $867 \cdot g^{-1}$ for 3.5 and 9.0 kg fish) and this study ($119 \cdot g^{-1}$ and $769 \cdot g^{-1}$ for 2.1 and 13.0 kg fish), and using predictive equations (Table 10). Comparing the range of point estimates, the three studies are similar, however our findings agree more closely with Erickson and Grossman (1986) when the comparison is based upon predictive equations. The inconsistency in the comparison is because Morse (fn. 9) used a linear equation, thus assuming that egg production per gram of body weight was constant for all body weights, and Erickson and Grossman (1986) and this study chose curvilinear equations. It is possible to conclude that small tilefish, like some other fishes (Grimes 1987), produce fewer eggs per unit body weight than larger fish.

We compared numbers of ova actually found in ripe ovaries collected on 1 July ($n = 3$) and 28 August ($n = 6$) to ovarian egg numbers predicted for the same size females to estimate what proportion of ova had been spawned in the mid- and late-spawning season. The analysis suggested that approximately 25% of ovarian eggs were spawned by July and 50% by the end of August. The ovaries of two postspawning females collected on 10 October contained considerable quantities of ovarian eggs >0.15 mm in diameter. These ova accounted for 15–20% of the predicted ovarian egg number. By December 11 ($n = 3$) the number of ovarian eggs >0.15 mm in diameter had decreased to about 5% of the predicted maximum ovarian egg number. Since atretic ova were observed in histological preparations of ovaries in spent and resting stages, and resorption is well documented in other teleosts (Hoar 1957; Smith 1965; Combs 1969; Foucher and Beamish 1977; LaRoche and Richardson 1980; Waltz et al. 1982), it seems reasonable to conclude that at least 15–20% of the maximum ovarian egg number are never spawned and are resorbed during the winter.

Sexuality

Our results agree with Erickson and Grossman (1986) that tilefish are gonochoristic and that secondary gonochorism is a possibility. Gonad microstructure and development of adult (>50 cm FL) tilefish were typical of most male and female oviparous teleosts, and identical to that described for

TABLE 10.—Comparison of ovarian egg number and relative ovarian egg number for small (2.0 kg) and large (9.0 kg) female tilefish calculated following Erickson and Grossman (1986), Morse,[1] and this study.

	Body weight	Egg number	Relative egg number
Erickson and Grossman	2.0	828,723	414
	9.0	7,875,326	875
Morse	2.0	1,773,003	887
	9.0	7,982,003	887
This study	2.0	917,434	459
	9.0	8,498,245	944

[1]Morse, W. W. Length, weight, spawning and fecundity of the tilefish, *Lopholatilus chamaeleonticeps*, from New Jersey waters. Unpubl. manuscr. Northeast Fish. Cent. Sandy Hook Lab., Natl. Mar. Fish. Serv., NOAA, Highlands, NJ 07732.

male and female *Caulolatilus microps* (Ross and Merriner 1983) and female *Lopholatilus chamaeleonticeps* (Erickson et al. 1985). Like Ross and Merriner (1983) and Erickson and Grossman (1986), we also found a few adult males (2 of 50) with ovigerous tissue (previtellogenic residual oocytes) in the testicular mass. Histological sections of testes revealed no gross structural features that indicated prior functional female status (e.g., remnants of an ovarian lumen (Sadovy and Shapiro 1987)). Furthermore, no ovary was ever observed in transition to a testis (transitional ovotestes), however transition can occur within a matter of weeks. Similar to other branchiostegids (*C. microps*, Ross and Merriner 1983; *Branchiostegus wardi* and *B. serratus*, Dooley 1978; *L. chamaeleonticeps*, Erickson and Grossman 1986), sex ratios were skewed in favor of males at large sizes. However, both sexes were present at most sizes and ages (45–95 cm FL and 5–10, 16, and 19 years) and only females were present at ages 29–36 years, ruling out protogyny. Disparate sex ratios at size are apparently due to differential growth and mortality rates between sexes (Turner et al. 1983; Harris and Grossman 1985).

Our histological examination of juvenile gonads suggest that some *L. chamaeleonticeps* may undergo prematurational sex reversal. All juvenile gonads examined (63 fish, 146–400 mm FL) appeared to be female, based upon gonad cell structure (i.e., presence of only oogonia and previtellogenic oocytes). We are very tentative about the determination that all of these small fish (<400 mm FL) were females, because undifferentiated gonia, oogonia, and spermatogonia are very similar in appearance (Yamamoto 1956; Hoffman 1963; Hyder 1969; Ross 1978). Once a gonad has developed gross structure such as spermatogenic tubules and crypts, or an ovarian lumen, determining sex is straightforward. We found residual oogonia in 2 of 50 histologically examined testes. We found no juveniles with truly intersexual gonads, nor were we able to observe a lumen. Ross and Merriner (1983) suggested that the confamilial *C. microps* underwent prematurational sex reversal, and that gonochorism in *C. microps* might be a regression from monandric protogyny. Their conclusions were based upon findings from four juveniles (one specimen with a totally ovarian gonad and the remaining three with gonads that contained substantial amounts of testicular tissue), and adult males (8 of 41 examined) with residual oocytes in the testicular mass.

That prematurational sex reversal has been observed among several families and species of fish suggests that either prematurational sex reversal is more common among fishes than suspected, or that early gonad development in fishes involves an all-female or female-appearing stage. For example, the salmonid *Salmo gairdneri* (Mrsic 1923); the cyprinids *Brachydanio rerio* (Takahashi 1977), *Barbus tetrazona* (Takahashi unpubl. data cited in Takahashi 1977), *Rodeus ocellatus* (Shimizu 1979), *Cyprinus carpio* (Davis and Takashima 1980), and *Carassius auratus* (Stromsten 1931; Takahashi and Takano 1971); and the anabantids *Macropodus concolor* and *M. opercularis* (Schwier 1939) are hatched as all females having ovaries with no testicular characteristics. About one-half continue normal development to mature females and about one-half undergo a transitory intersexual stage before becoming adult males. The female juvenile cyprinids *Brachydanio rerio*, *Barbus tetrazona*, *Rhodeus ocellatus*, and *Carassius auratus* all develop an ovarian lumen, as well as oogonia and previtellogenic oocytes. Prematurational sex change is reportedly common among the hermaphroditic Sparismatinae (Scaridae) that spend their entire life as males (Robertson and Warner 1978).

Social Control

We interpret the data on sexual maturity and sexual dimorphism to suggest that some sexually mature males delay participation in spawning for up to 3 years and 10–15 cm, and that this mating system is socially mediated. Histological assessments of sexual maturity revealed that both males and females produced mature gametes by about 50 cm FL and 5–6 years. However, visual inspection of gonads to determine maturity gave the same result as the histological evidence in females, but indicated that males were not mature until attaining 65–70 cm FL and 7–8 years. Ross and Merriner (1983) also reported that some *Caulolatilus microps* males that were visually assessed as immature were later shown by histological methods to be producing mature gametes, and Erickson and Grossman (1986) found *L. chamaeleonticeps* off Georgia that showed active, yet incomplete spermatogenesis.

Sexual dimorphism in tilefish is manifested in the size of the adipose flap which is conspicuously larger in males than females and larger ultimate body size in males; size of the adipose flap may be an indication of male breeding status. The adipose flap of males became larger at 65–70 cm FL (7–8 years) when males were judged sexually mature by visual inspection (i.e., had developed large testes), not

when they were functionally mature at 50 cm FL as revealed by histological methods.

A nonrandom mating system of pairing, involving mate selection by females, is consistent with the both sexual dimorphisms observed in tilefish. Female mate selection can convey a reproductive advantage to large males (Ghiselen 1969; Howard 1979), but in randomly mating species, females are usually larger than males (Ghiselen 1969). Female ability to discriminate males is required to support female mate selection (Howard 1979), which often leads to development of specialized structures and colorations by males for display (Krebs 1972; Warner and Robertson 1978). The enlarged adipose flap in tilefish certainly represents a conspicuous, highly visible feature in some adult males that could serve as a visual cue to signal male breeding status.

The evolution of a female mate selection system requires that a male have the ability to control resources important to the female (Howard 1979; Krebs and Davies 1984), and several lines of evidence suggest that male tilefish may be territorial. Burrowing is apparently the rule in the family (Able et al. 1987). Direct observation from submersibles and mark-recapture data indicated that tilefish orient to particular burrows, and may be long-term residents of their habitats (Grimes et al. 1983, 1986). Furthermore, time-lapse photography showed the same male-female pair of tilefish utilizing the same burrow over a 26-h period (Grimes et al. 1986), and pair formation has been observed in the branchiostegids *Malacanthus plumieri* (Clark and Ben-Tuvia 1973), *Hoplolatilus* sp. (Thresher 1984), and *H. starcki* and *H. cuniculus* (Randall and Dooley 1974).

We believe that our data indicate that tilefish have a mating system consisting of two classes of sexually mature males, a category actively engaged in spawning and a category of satellite males that do not spawn. Similar breeding systems have been described for several species of hermaphroditic reef fish (Popper and Fishelson 1973; Fishelson 1975; Warner and Robertson 1978; Robertson and Warner 1978; Warner and Hoffman 1980; Shapiro 1984). For example, there are scarid and labrid populations with large territorial terminal phase males that have preferred mating status, and nonterritorial initial phase males that have nonpreferred breeding status (Warner and Robertson 1978; Robertson and Warner 1978). Hermaphroditic populations of the serranid *Anthias squamipinnis* in the Gulf of Eilat have two behaviorally distinct types of males, a dominant territorial male that actively courts, interacts, and spawns with females, and smaller males that do not interact or spawn with females in the social group. The latter male category have filamentous degenerative gonads (Popper and Fishelson 1973; Fishelson 1975). These mating systems are characterized by strong sexual selection and maintenance of reproductive territories by males, and by being reef systems in which fish are habitat limited. Tilefish are also severely habitat limited, i.e., to burrowable clay substrate generally (Able et al. 1982; Grossman et al. 1985; Grimes et al. 1986).

During the period we studied reproduction, the fishery for tilefish was rapidly expanding, and one effect of fishing seems to have been to alter the structure of the mating system. Based upon both age-structured and non-age-structured population modeling, tilefish population density was reduced by about one-half to two-thirds from 1978 to 1982, apparently due to the rapid expansion of the commercial longline fishery (Turner 1986). Female size, and particularly age, at maturity do not seem to have been altered in any consistent fashion by the population reduction from fishing. Males, on the other hand, appear to have experienced profound changes in visually assessed maturity; they clearly were mature at smaller size (10 cm) and younger age (2–2.5 years) in 1982 than in 1978.

We interpret the decrease in size/age of maturity in males to be the effect of fishing. Fishing lowered population density, and in so doing may have made mating territories available to smaller and younger males. This interpretation is supported by the findings of Warner and Robertson (1978) and Robertson and Warner (1978) that the ratio of the two categories of sexually mature males (initial and terminal phase) in western Caribbean scarid and labrid populations was density dependent; i.e., relatively more initial phase males were found in dense populations.

ACKNOWLEDGMENTS

Our tilefish research was initiated at the suggestion of the late Lionel A. Walford. We tender grateful appreciation to the following individuals and institutions for their assistance in this research. Joseph Desfosse, Susan Shepherd, Gary Shepherd, and Stuart Katz helped extract data from samples. Richard Trout and Bruce Babiarz provided statistical and histological advice, respectively. Fran Puskus, Louis Puskus, John Larsen, and the fishermen of Barnegat Light and Sea Isle City, NJ cooperated in obtaining tilefish samples. Daniel Erickson

and an anonymous reviewer provided useful editorial comments. Support for this research was provided by New Jersey Sea Grant (RF-2), the New Jersey Agricultural Experiment Station (AES 12409), and the Center for Coastal and Environmental Studies, Rutgers University.

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A FIELD METHOD FOR DETERMINING PREY PREFERENCE OF PREDATORS

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ABSTRACT

A new field method for determining prey preferences of fish that feed on juvenile salmon is described. The basic elements of this method consist of capturing, tagging or marking, and releasing prey with known characteristics, and comparing these characteristics with those of tagged prey subsequently recovered from the stomachs of predators. The feasibility of this approach is illustrated by two experiments conducted in 1985, designed to assess prey size preferences of predators feeding on juvenile pink salmon during the early sea-life period. The results indicate that yearling coho salmon, *Oncorhynchus kisutch*, were size selective when feeding on juvenile pink salmon, *O. gorbuscha*, preferring the smaller prey. A major advantage of this method is that it eliminates the need to determine the abundances of various prey types in the field. It also allows the investigator to control or precisely measure many of the variables that are known to affect the availability of prey to predators.

Predation plays an important role in shaping the ecological structure of many biological systems. One aspect of predation that has attracted considerable interest is the observation that, when offered a choice of prey types, predators typically show a preference for one of them. The result is that more of the preferred prey are consumed than would be expected, based on the relative abundances of the various prey types.

There have been many attempts to quantify the food or prey preferences of predators (e.g., Hess and Swartz 1940; Ivlev 1961; Schneider 1981) using a wide variety of mathematical indices of preference (reviewed by Cock 1978; Pearre 1982). In some situations, however, this approach clearly is not suitable. For example, in many systems the relative abundances and species composition of the prey can vary substantially over the normal feeding range of the predators. This is particularly evident in fisheries, where piscivorous predators and their prey are often very mobile, and can travel considerable distances during even a single feeding period. In such cases, the proportions of the various prey found in the stomachs of predators may result from variations in the relative concentrations or availability of prey over the extensive area searched by the predator, rather than from any prey preference. It is typically very difficult to determine the concentrations and species composition of prey over such large areas, so indices of preference may not provide much insight into the predation process.

The purpose of this paper is to describe a new method for determing the prey preference of predators in the wild. This method consists of a field experiment in which a number of potential prey with known characteristics are released. These prey are tagged prior to release to allow positive identification even if they mix with other prey of the same type after they are released. The prey preference of the predators is assessed directly by comparing the characteristics of the tagged prey found in the stomachs of predators with those of the prey that were released. The major advantage of this approach is that the relative abundances and other characteristics (species ratios, size composition, etc.) of the various prey types are known in advance and additional field measurements are not required. In addition, if only tagged prey are compared, there is much less ambiguity in assessing the preference of predators for each type of prey because the major alternative explanations are eliminated. Although applicable to a wide variety of predator-prey interactions, the details and potential utility of this method are illustrated by two experiments conducted in Masset Inlet and Masset Sound, B.C., Canada. In both cases the goal was to test the hypothesis that natural fish predators were size selective when feeding on juvenile pink salmon, *Oncorhynchus gorbuscha*, during the early sea-life period.

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Manuscript accepted July 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

METHODS

The first experiment was conducted on 26 April and the second experiment during 6 and 7 June 1985. Pink salmon fry were captured in the Yakoun River during 10–18 April using two inclined plane traps with mouth openings of 1.1 m^2. The traps were emptied each morning and the pink salmon transferred by truck to several 1 m^3 net pens attached to the research vessel *Velella*, anchored at Marinelli Point (Fig. 1).

All pink salmon were tagged and marked to allow positive identification after they were released. During 15–18 April 6,000 pink salmon were anesthetized with tricaine-methanesulfonate (MS-222) and tagged with half-length binary-coded wire tags by an experienced tagging crew. Proper placement of each tag was confirmed by passing all fish through

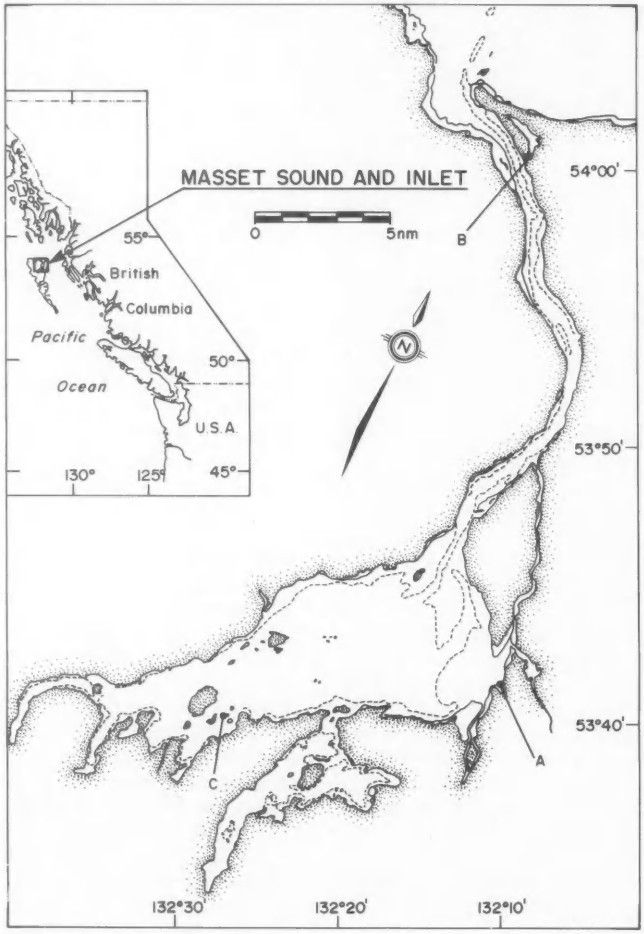

FIGURE 1.—Chart of Masset Inlet showing locations of first (Marinelli Point) (A) and second (B) releases of tagged fish and saltwater enclosure (C) used to hold tagged fish until required for the second experiment.

a 2.54 cm (1 inch) diameter Quality Control Device (QCD), manufactured by Northwest Marine Technology[2] (Shaw Island, WA 98286). Samples of tagged fish were also dissected and examined visually and microscopically to verify tag implantation. Three thousand of these pink salmon were also marked externally by amputating either the left or right pectoral fin. No other fins were amputated. The purpose of the fin clipping was to determine which method (nose tag or fin clip) was more effective for identifying fish recovered from the stomachs of predators.

After tagging and marking, all pink salmon were transferred back into the small, saltwater enclosures. On 20 April the three thousand tagged but unmarked pink salmon were transferred to a larger (51 m^3) enclosure anchored near the southwest end of Masset Inlet, and held until required for the second experiment. This enclosure was shallowed by hand once each week to check the condition of the fish and cleaned with a high-pressure hose every 10–14 days to remove algae growing in the meshes. The food supply of the pink salmon held in this enclosure was not controlled and consisted of whatever came through the meshes. No supplementary food was added. Under this regime the pinks remained very active and appeared healthy.

The first experiment was initiated at 1600 on 26 April, by releasing 3,000 tagged and fin-clipped pink salmon at Marinelli Point. A sample of 99 fish was removed, anesthetized with 2-phenoxyethanol, and the live fork length of each fish measured to determine the size distribution of fish at the time of release. A single beach seine set was made three hours later, in the immediate vicinity of the release site, to collect a sample of potential predators.

The second experiment was initiated by releasing 1,800 tagged pink salmon at 1130 on 6 June, into the boat harbor at Masset (Fig. 1). None of these fish were fin-clipped. A sample of 100 pink salmon was removed prior to the release, and each fish measured to determine the size distribution of fish at the time of release. Two beach seine sets were made to collect potential predators prior to the time of release, the first at 0930 and the second at 1015. A total of sixteen additional sets were made after the release, seven between 1245 and 1826 on 6 June, and nine more between 0900 and 1400 the following day.

[2]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

The beach seine used to capture potential predators was 46 m long and constructed of 6.4 mm stretched nylon mesh. All potential predators were examined immediately after capture. Each measured fish was anesthetized in 2-phenoxyethanol, and the stomach contents obtained by either hydraulic flushing or dissection. All fish remains in the stomach contents were examined visually or microscopically to identify prey to the species level, using Hart (1973) as a general reference and Phillips (1977) to identify juvenile salmon. All juvenile salmon found in the stomachs of predators and any live juvenile salmon captured along with the predators were measured (if possible), examined for missing fins, and passed through the QCD several times to determine if they were tagged.

Yearling coho salmon, *Oncorhynchus kisutch*, captured on the first day of the second experiment were used to obtain an estimate of the total population of coho salmon in the vicinity of the release site. All coho salmon captured on 6 June were retained, anesthetized with 2-phenoxyethanol, and marked using a hot-wire branding device. At 2000 on 6 June, these coho were sorted to remove any that did not appear healthy and fully recovered, and the remaining 170 were released. All coho captured the following day were inspected to determine if they were marked. The numbers of marked and unmarked coho were used to derive a simple (single census) Petersen estimate of the total population of yearling coho salmon in the vicinity of the release site using the following equation (Ricker 1975):

$$N = \frac{(M + 1)(C + 1)}{(R + 1)} \quad (1)$$

where N = total number of coho salmon at time of marking
M = number of coho salmon marked and released on 6 June
C = total number of coho salmon captured on 7 June
R = number of marked coho salmon recaptured on 7 June.

The 95% confidence interval for the population estimate was obtained by substituting into this equation the fiducial limits of the number of recaptured coho salmon, from tables of the Poisson distribution (Ricker 1975). These figures were used to estimate the total number of tagged pink salmon eaten by coho salmon in the second experiment, using the equation

$$T = (P * N)/E \quad (2)$$

where T = total number of pink salmon eaten
P = total number of pink salmon in all stomachs examines
N = estimated total population of coho salmon, from Equation (1)
E = total number of stomachs examined.

RESULTS

The 3,000 tagged and marked pink salmon released at Marinelli Point on 26 April ranged in size from 34 mm to 41 mm, with an average of 38 mm (Table 1). A total of 57 juvenile sockeye salmon (*Oncorhynchus nerka*), 5 pink salmon, 2 chum salmon (*O. keta*), 4 starry flounder (*Platichthys stellatus*), 1 sturgeon poacher (*Agonus acipenserinus*), and 210 yearling coho salmon were captured in the single beach seine set done after the tagged fish were released. All five pink salmon had been fin-clipped and tagged. Three of these pinks had fork lengths of 37 mm and the other two were both 38 mm long. The two chum salmon had fork lengths of 41 mm and 40 mm. The four starry flounders and single sturgeon poacher were all small and were immediately released. All 210 coho salmon were measured and their stomach contents examined for evidence of predation on juvenile pink salmon. A total of 90 coho salmon had remains of fish in their stomachs, including 51 pink salmon, 1 chum salmon, and 14 juvenile salmon that could be identified only as either pink or chum salmon, due to extensive digestion (Table 2). One additional coho salmon had eaten two Pacific sandlance, *Ammodytes hexapterus*, but all other fish remains were too digested to positively identify. Out of the 23 tagged pink salmon found in the stomachs of these coho salmon, only 18 were sufficiently intact to permit measurements of their fork length (Table 2). The average length of these pink salmon was significantly less ($t = 8.02$; $P < 0.001$) than the average length of the pink salmon that were released (Fig. 2). Twelve of the eighteen tagged and measurable pink salmon found in the stomachs of the coho were clearly missing a pectoral fin. The pectoral fins of all the other fish were too digested to be certain whether or not they had been fin-clipped. The average length of the 12

TABLE 1.—Characteristics of tagged juvenile pink salmon released in each experiment and those subsequently recovered by beach seining. Nr = no. released; Ns = no. fish in prerelease sample; Min = minimum fork length; Max = maximum fork length; $\bar{X}$ = mean fork length; C.I. = 95% confidence interval for $\bar{X}$; Nc = no. of tagged salmon recaptured by beach seining; H = no. hours after release of tagged fish.

	Tagged fish released							Tagged fish recaptured						
Date	Species	Nr	Ns	Min	Max	$\bar{X}$	C.I.	Species	Nc	Min	Max	$\bar{X}$	C.I.	H
4/26/85	pink	3,000	99	34	41	38.1	37.9–38.4	pink	5	37	38	37.4	36.7–38.1	1.5
6/6/85	pink	1,800	100	36	51	44.4	43.8–44.9	pink	3	42	46	44.3	39.2–49.5	1–3
								pink	12	40	50	44.7	42.7–46.6	3–5
								pink	4	40	47	42.8	38.0–47.5	5–7
								pink	0	—	—	—	—	21–26

TABLE 2.—Number and size of juvenile salmon found in stomachs of predators in each experiment. Sets = no. beach seine samples; S = no. of stomachs examined; N = total no. juvenile salmon in stomachs; Nc = no. of tagged fish in stomachs; Nm = no. of tagged fish whose fork length could be measured; Min = minimum fork length; Max = maximum fork length; $\bar{X}$ = average fork length; C.I. = 95% confidence interval for $\bar{X}$; JS = juvenile pink or chum salmon.

					Juvenile salmon found in predator stomachs							
					All salmon		Tagged salmon only					
Experiment	Date	No. sets	Predator	S	Species	N	Nc	Nm	Min	Max	$\bar{X}$	C.I.
1	4/26/85	1	coho	210	pink	51	23	18	34	38	35.6	35.0–36.2
					chum	1	0					
					JS	14	0					
2	6/6/85	16	coho	374	pink	17	15	15	36	45	40.7	39.3–42.1
			staghorn	24	pink	0						
			Dolly Varden	15	pink	0						

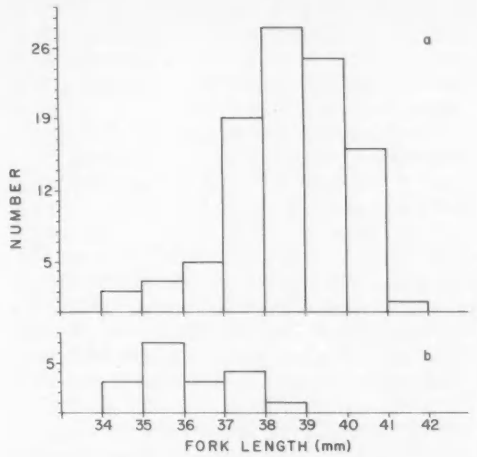

FIGURE 2.—Size-frequency distribution of sample of tagged pink salmon released in the first experiment (A) and all tagged pink salmon subsequently recovered from stomachs of predators (B).

fin-clipped fish was 35.4 mm, which is not significantly different ($t = 0.47$; $P > 0.50$) from the average length of the 18 tagged and measurable pink salmon.

Pink salmon released in the second experiment ranged in size from 36 to 51 mm fork length, with an average of 44.4 mm (Table 1). A total of 1 juvenile sockeye salmon, 1 juvenile chum salmon, 28 yearling coho salmon, 6 Pacific staghorn sculpin (*Leptocottus armatus*), 10 Pacific herring (*Clupea harengus pallasi*), approximately 500 larval walleye pollack (*Theragra chalcogramma*), 20 Pacific snake prickleback (*Lumpenus sagitta*), 1 red Irish lord (*Hemilepidotus hemilepidotus*), 6 Dolly Varden (*Salvelinus malma*), and 10 starry flounder were captured in the 2 beach seine sets done before the release. Examination of the stomach contents of all the coho salmon, five staghorn sculpins, the red Irish lord, and all the Dolly Varden provided no indication that any of these fish had recently eaten juvenile pink or chum salmon. The seven additional beach seine sets done on 6 June after the release of the tagged pink salmon captured a total of 271 coho salmon, 33 Dolly Varden, 46 staghorn sculpin, 2 coastal cutthroat trout (*Salmo clarki clarki*), 55 pink salmon, and 3 chum salmon. Nineteen pink salmon had been tagged (Table 1). All the untagged pinks were larger.

The stomach contents of 246 coho salmon, 14 Dolly Varden, and 16 sculpins were examined. There was no evidence that any of the Dolly Varden or sculpins had eaten any juvenile pink or chum salmon, although one sculpin had eaten a juvenile coho salmon. However, 13 of the coho salmon had eaten a total of 17 juvenile pink salmon, of which 15 had been tagged. The head was missing from one of the two untagged pink salmon so it could not be measured, but the fork length of the other was 51 mm. The tagged pink salmon found in the stomachs of the coho salmon were typically the smaller ones (Fig. 3), with an average length significantly less ($t = 5.06$; $P < 0.001$) than the average length of all pink salmon that were released in this experiment (Table 2).

No juvenile salmon were found in the stomachs of predators captured on 7 June. A total of 1 juvenile pink salmon, 141 yearling coho salmon, 1 Dolly Varden, and 115 staghorn sculpins were captured in 9 beach seine sets. The pink salmon was not tagged and none of these predators had recently eaten any juvenile pink or chum salmon. Five of the coho salmon had been branded, so the estimated total population of coho salmon in the vicinity of the release site was 4,047, with a 95% confidence inter-

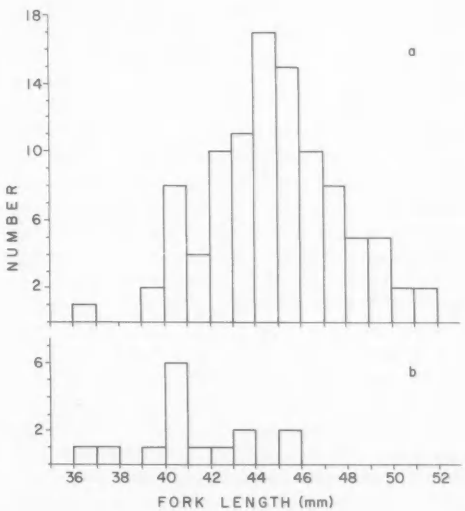

FIGURE 3.—Size-frequency distribution of sample of tagged pink salmon released in the second experiment (A) and all tagged pink salmon subsequently recovered from stomachs of predators (B).

val of 1,912 to 9,339. Based on these figures, it is estimated that coho salmon consumed a total of 162 (9%) of the tagged pink salmon released on 6 June, with a 95% confidence interval ranging from 76 (4%) to 375 (21%).

DISCUSSION

Determining the prey preference of predators in the wild is an important but difficult problem. The two experiments reported here illustrate a new approach to determining the selectivity of predators in the wild. Aside from logistic problems, the success of this method depends on the validity of four main assumptions: 1) predators that are captured and examined, and their stomach contents, are truly representative of the total predator population of interest; 2) tagging or marking the prey does not result in abnormal behavior of either the prey or predators; 3) ingestion and partial digestion of the prey by the predators does not significantly alter the characteristics of the prey that are of primary interest; 4) all of the tagged prey remain equally "available" to the predators for the duration of the experiment.

The first assumption should be valid if the sampling program is appropriately designed, considering the statistical tests that will be used to analyze the data. This is a complex topic and an in-depth discussion is beyond the scope of this paper. However, many extensive references are available (e.g., Anderson and McLean 1974; Cochran 1977; Montgomery 1976).

The two experiments reported here were designed only to demonstrate the utility of this approach and do not clearly show how generally applicable the results are. Only a small number of tagged fish were released and samples of predators were collected with a beach seine, which undoubtedly is biased to some degree in terms of the species and sizes of fish that were captured. In addition, the samples were collected at only one location in the first experiment and over a relatively small area in the second experiment. However, extensive sampling and examination of the stomach contents of fish predators over a 3-yr period indicates that yearling coho salmon are the major predators of juvenile pink salmon throughout Masset Inlet and Masset Sound (Hargreaves in press). The results of these two experiments are also consistent with those obtained from enclosure experiments, which indicate that yearling coho salmon are size selective when feeding on juvenile pink or chum salmon (Parker 1971; Hargreaves and LeBrasseur 1986). Thus, although quite limited in scope, these two experiments provided results that are consistent with those obtained by two other independent, but considerably more expensive and laborious, methods.

The assumption that tagging and marking the prey does not affect the behavior of predators or prey can be assessed either by direct observation or by conducting additional experiments. In some cases it may be possible to design the experiment to allow observation of both the predators and prey throughout the experiment and directly observe any unusual behavior. However, in many cases, additional experiments will probably be required. For the two experiments reported here, the pink salmon used in the first experiment were tagged and fin-clipped; the fish released in the second experiment were tagged but were not fin-clipped. The results of the first experiment indicate that tagging was more effective than fin-clipping for recognizing fish recovered from the stomachs of predators. In terms of behavioral changes, previous work indicated that the mortality of tagged and untagged juvenile salmon was not significantly different when exposed to predators and that tagging juvenile salmon had no noticeable affect on the behavior of either the predators or prey (Hargreaves and LeBrasseur 1986). However, the tagged fish used in these enclosure experiments were not fin-clipped.

Earlier studies have indicated that amputation of fins from juvenile salmon typically results in lower survival rates (Ricker 1949). Marked pink salmon fry also suffer higher mortality than unmarked fry, possibly due to a bias on the part of predators for marked prey (Parker et al. 1963). This is not a major concern in the two experiments reported here because the intent was to determine the size selectivity of predators, rather than any selectivity for marked or unmarked prey. In addition, fin-clipped pink salmon were used only in the first experiment but predators consumed significantly more of the smaller prey in both experiments. This supports the assertion that fin-clipping the pink salmon did not substantially affect the prey size selectivity of the predators. In general, the possibility that the results of these types of experiments may not apply to untagged or unmarked prey can be eliminated by using only tags or marks that are known to have negligible effects on the behavior of both the prey and predators.

The third assumption, that ingestion and partial digestion of the prey by the predators does not significantly alter the important characteristics of the

prey, can often be directly verified. For the two experiments reported here, prey size (fork length) was the characteristic that was most important. The observed difference between the average length of the tagged prey that were released and the tagged prey subsequently recovered from the stomachs of predators was 2.5 mm (6.6%) in the first experiment, and 3.7 mm (8.3%) in the second experiment. These are small differences, and the possibility that they might be due to experimental error rather than predator selectivity must be considered. All length measurements were made to the nearest millimeter and numerous remeasurements indicated that measurement errors were negligible at this level of accuracy. To eliminate the possibility that the length of the tagged fish might decrease if they were preserved (Parker 1963), live fish were used to determine the length-frequency distribution of the prey prior to release and all prey recovered from the stomachs of predators were immediately measured. Burgner (1962) reported that the length of sockeye salmon smolts decreased by 2–3% because of *rigor mortis* alone. However, experiments conducted in Masset Inlet in 1984 indicated much smaller changes occur after death in juvenile pink salmon. At temperatures of 9°–10°C, the average length of 26 juvenile pink salmon of known length, fed to and subsequently recovered from the stomachs of 19 yearling coho salmon, decreased less than 1% for periods of up to four hours after ingestion (Hargreaves unpubl. data). In the two experiments reported here, numerous beach seine sets were made to capture potential predators, but all of the tagged pink salmon found in their stomachs were recovered within four hours of the releases of tagged prey. Shrinkage of the prey after ingestion therefore can account for only a small portion of the observed differences in size between the prey that were released and those that were found in the stomachs of predators.

The fourth assumption, that all tagged or marked prey remain equally "available" to predators throughout the experiment, will usually prove to be the most difficult to assess and verify. The availability of prey to predators frequently depends on characteristics of the predators (hunger level, visual acuity, mobility, body or gape size, individual or group behavior, etc.), the prey (abundance, coloration, size, speed, endurance, behavior, etc.), and the environment (habitat complexity, light conditions, etc.). These parameters can interact in a complex manner, so that it is typically only in the simplest situations that all factors that affect the availability of prey to a predator can be thoroughly investigated and understood (Curio 1976; Zaret 1980).

Predators consumed significantly more of the smaller prey in both experiments reported here, despite substantial differences in the physical characteristics of the two release sites, time of year, and various characteristics of the predators (abundance, species composition, size, feeding history, etc.). This suggests that the availability of prey to the predators was not substantially affected by variations in the characteristics of either the predators or the environment. It also appears reasonable to assume that prey of all sizes remained equally available to predators during both experiments. All of the tagged prey were one species and received identical treatment prior to release. There is no reason to think there were any substantial differences in the physical characteristics among the prey at the time of release, aside from the desired variation in size.

It is conceivable, however, that differences in prey behavior or size might have indirectly influenced the availability of prey to the predators. For example, extensive sampling of juvenile salmon in Masset Inlet has indicated a tendency for larger pink salmon to be concentrated further offshore than smaller pink salmon during the early sea-life period (Hargreaves et al. 1987a, b). Swimming speeds of salmon are also known to increase rapidly with increasing body size (Brett 1965). Thus, if there was any tendency for tagged salmon to rapidly swim away from the release sites, larger fish may have left quicker than smaller fish. The result could be a decrease in the average size of tagged salmon found in the immediate vicinity of the release site and the incorrect conclusion that predators were selectively feeding on the smaller prey.

In fact, however, this possibility appears unlikely. In both experiments the size of the live, tagged fish recovered along with the predators was not significantly different than the size of the fish that had been released as much as nine hours earlier (Table 1). There is also no indication that the mean size of these fish changed in a consistent manner over the course of the second experiment. These results suggest that, if there was any segregation of tagged prey after release, it was probably minor and did not appreciably affect the availability of prey to the predators.

In general, complications arising from variations in the availability of prey to the predators may be reduced or eliminated by limiting the duration of the experiment. If all of the prey are released at one time and location, it is reasonable, and in most cases

probably valid, to assume that all prey are equally available to any predators captured in the immediate vicinity a short time later. The amount of time during which the prey subsequently remain equally available to predators will likely vary from one situation to the next. If the prey are very mobile, probably some will eventually become less or more accessible to predators than others. This possibility can be eliminated or at least minimized by keeping the experiment short enough to ensure that the prey do not have sufficient time to segregate or move away from the release site. The magnitude of this problem and thus the appropriate duration for each experiment may be assessed by recapturing some of the tagged prey after the release. The experiment should be terminated when the characteristics of the recaptured prey begin to diverge significantly from those of the original prey population.

Determining the prey preference of predators in the wild is a concern to many biologists. All methods of determining the prey selectivity of predators in the wild are, and will likely continue to be, hampered by the complexity of the related problem of determining the relative "availability" of prey to predators. The advantage of the method proposed here is that it allows the investigator to control some of the major variables that are known to affect the availability of prey. The most important characteristics of the prey (species ratios, abundance, size ranges, etc.) can be determined before any predation occurs and in many cases can also be precisely controlled. The predators remain free to feed on all types of prey in the study area, but for the purposes of the investigator, the choice of prey can effectively be reduced to those with known characteristics and origin. This is a major advantage when compared with the more traditional approach of calculating selectivity indices, as it eliminates the need to determine the relative abundances of prey in the field. It also substantially reduces the ambiguity associated with interpreting selectivity indices for highly mobile predators, where typically there is little or no information available concerning the area traveled by the predator during the feeding period and thus what prey were actually available to the predator.

The specific goal of the two experiments reported here was to determine if predators were size selective when preyir g on juvenile pink salmon during the early sea-life period. The results indicate that yearling coho salmon were the dominant predator of juvenile pink salmon at two locations, one in Masset Inlet and the other in Masset Sound, and that the average size of juvenile pink salmon consumed by these predators was significantly less than the average size of pink salmon that were released. These results are consistent with those obtained from two other independent approaches and suggest this method may be a viable and cost-effective alternative for determining the prey preferences of predators in the wild. It may be particularly useful for assessing prey preferences of predators feeding on juvenile salmon near hatchery facilities in Canada and the United States, where millions of juvenile salmon are currently tagged and released each year.

ACKNOWLEDGMENTS

Suggestions and comments from an anonymous reviewer are greatly appreciated. Robin LeBrasseur and Owen Kennedy assisted with the supervision of the field experiments and analyses of the stomach samples. Bruce Patten, Lui Marinelli, Tom Poole, Josette Weir, Rick Hobbs, Ted Carter, and Bob Hungar helped to capture, tag, and sort the juvenile salmon and assisted in the beach seining and processing of samples collected in the various experiments. Trans-Provincial Airlines generously permitted unlimited use of their seaplane wharf and other facilities at Masset, B.C. to conduct the second experiment during 6 and 7 June 1985.

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EXPERIMENTAL MANIPULATION OF POPULATION DENSITY AND ITS EFFECTS ON GROWTH AND MORTALITY OF JUVENILE WESTERN ROCK LOBSTERS, *PANULIRUS CYGNUS* GEORGE

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ABSTRACT

A density manipulation experiment was conducted at Seven Mile Beach, Western Australia, to compare growth and mortality for different density groups of juvenile western rock (spiny) lobsters, *Panulirus cygnus*, inhabiting limestone patch-reefs. Juveniles on a control reef were left at their natural, high densities while those on a treatment reef were reduced to approximately 25% of the original, natural density by trapping and reintroduction, which maintained the original size-frequency distribution. Mark-recapture studies were conducted on each reef at three monthly intervals for a year to estimate size-specific growth rates, population densities, and mortality rates. Direct counts of individuals were made by divers to estimate total numbers of juveniles on each reef. There were no statistically significant differences in growth rates for any age category between the control and treatment reefs, but there were significant differences in size-specific mortality rates between the treatment and control groups, with much lower mortality on the treatment reef. Our results suggest that markedly reduced densities of juveniles on a reef may lead to a corresponding reduction in mortality, but no effect on growth was evident. However, part of the apparently higher mortality on the control reefs may instead have been due to emigration of tagged individuals to other reefs. The difficulties of conducting manipulation experiments in the field on a highly mobile species are discussed.

The western rock (spiny) lobster, *Panulirus cygnus*, occurs on the coast of Western Australia from North West Cape (lat. 22°S) to Cape Naturaliste (lat. 34°S). Juveniles (2–5 years old) inhabit the coastal limestone reefs, primarily at depths of 1–10 m (Chittleborough and Phillips 1975). They remain on the reefs for several years, apparently with little movement from one area to another (Chittleborough 1974a). Joll and Phillips (1984) found that the juveniles feed on a variety of animals and plants associated with the seagrass beds surrounding the reefs. Following the spring molt, larger animals (ages 4–6) move to the adult habitats in depths of 30–150 m (Morgan et al. 1982).

Chittleborough (1970) observed that, near the center of the geographical range, recruitment of small juveniles appeared to exceed the holding capacity of the reef system. He concluded that density-dependent mortality of the juveniles at such sites limits their recruitment to the adult stock. He also observed reduced growth rates of animals at these sites and considered that the available food resources may be inadequate for the maintenance of optimum growth at such high densities.

Although there have been many field studies on the ecology of spiny lobsters (see review by Kanciruk 1980), none have attempted experimental manipulation to elucidate the effects of population density on growth and survival. This paper considers the growth and survival of juvenile *P. cygnus* inhabiting experimental and control patch-reefs at Seven Mile Beach, following a manipulation designed to reduce the density of juveniles of the experimental reef. The hypothesis to be tested was that high population densities of juvenile lobsters limit the growth and survival of the western rock lobsters. Despite its inherent practical problems, a manipulation approach was adopted as the one most likely to yield direct evidence to evaluate the hypothesis.

Manipulation experiments are best done using replicated experimental areas and both increases and decreases in the density of the species under consideration (Connell 1974; Underwood 1979). However, where species (such as lobsters) cannot be transplanted or enclosed effectively, the only practical option is to simply reduce densities (Connell 1983). In the case of the study described here, there are also practical limitations in finding sufficiently

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Manuscript accepted June 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

similar experimental areas to employ as replicates and in selecting control reefs which are equivalent to the premanipulation condition of experimental reefs. In this experiment juveniles on one reef, selected as the control site, were left at natural, high densities, while those on another, selected as the treatment site, were reduced to approximately 25% of their original, natural density. A third reef, also left at its natural high density, was monitored at a lower level to examine the degree of representativeness of the control.

METHODS

Reef Study Sites

Three limestone patch-reefs at Seven Mile Beach, Western Australia (lat. 29°08′S; long. 114°54′E), designated as reefs I, III, and V (Fig. 1), were used as the study sites. These three test reefs are typical of those at Seven Mile Beach in terms of both their structure and biota. Observations by divers also indicated that the size structure of *P. cygnus* on each reef was similar. The patch-reefs occupy a lagoon environment between the beach and a limestone barrier reef approximately 400 m offshore. Each patch-reef is surrounded by a calcareous, sandy substrate and areas of limestone, which both support extensive seagrass beds of mixed species composition, the primary feeding areas for juvenile *P. cygnus* (Cobb 1981; Joll and Phillips 1984). Seagrass species of the genera *Amphibolis*, *Heterozostera*, and *Halophila* dominate in these beds. The reefs themselves are covered by *Amphibolis* spp. and by a variety of algal species.

The approximate area of reef III, the treatment reef, is 0.104 ha, and that of reef V, the main control reef, is 0.103 ha. Reef I, the secondary control reef, has an area of approximately 0.071 ha. Reef I is located approximately 750 m south of reef V, while reef III is located approximately 60 m directly west and offshore from reef V (Fig. 1). Adequate separation of the treatment and control reefs from each other for the purposes of the experiment was assumed, based on maximum foraging ranges of up to 50 m for *P. cygnus* in the Seven Mile Beach area reported by Chittleborough (1974a). Water depths are 2–3 m around reefs I and V and 3–5 m around reef III. The tops of the reefs are nearly exposed at low tide.

Single Molt Increments, Annual and Seasonal Growth

The numbers of juvenile *P. cygnus* from each reef which were sexed, measured, and marked or re-

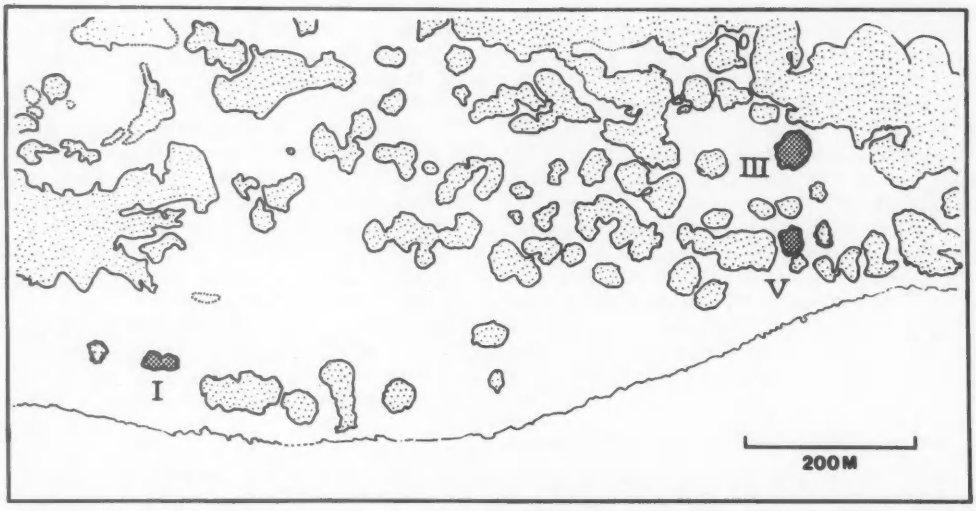

FIGURE 1.—Map of study area at Seven Mile Beach, Western Australia, showing the locations of reefs, I, III, and V (dark shaded) in relation to other reefs (light shaded).

moved in January 1981 at Seven Mile Beach are given in Table 1. Animals with carapace lengths (CL) ≥40 mm were marked with individually numbered western rock lobster tags (Chittleborough 1974b). Animals with CL <40 mm were marked with individually numbered Floy[4] No. FD-68B spaghetti tags (Davis 1978). Growth data were obtained from tagged individuals recaptured on the three test reefs during resampling in February, March, May, August, and September 1981, and January and February 1982. Growth of tagged *P. cygnus* between recaptures over the period January to May was used to provide data on single molt increments.

Size and Age Structure

Age classes were identified from length-frequency distributions, as described by Chittleborough (1970) and Chittleborough and Phillips (1975). From analysis of the size structure present in January 1981, juveniles up to 38.0 mm CL were judged to be 2 years of age at that time; 38.1–55.0 mm, 3 years of age; 55.1–68.0 mm, 4 years of age; and those >68.1 to be 5 years of age or older. Similarly for January 1982, animals up to 42.5 mm CL were considered to be 2 years of age at that time; 42.6 mm–55.0 mm, 3 years of age; those 55.1–68.0 mm to be 4 years of age; and those >68.1 to be 5 years of age or older.

Population Size, Density, and Mortality Rates

Estimates of the population size, density, and mortality rates of *P. cygnus* juveniles on reef I have been made at Seven Mile Beach since 1970, using recaptures from baited traps (Chittleborough 1970; Chittleborough and Phillips 1975). These estimates for reef I were continued during the period of this study on reef I and, in addition, estimates were also undertaken for reefs III and V, using the same traps and mark-recapture methods. In the present study, 12–13 traps were set around the perimeter of each test reef to ensure catches directly from the area of the reef. At each sampling time an array of 12–13 traps was set simultaneously around reefs III and V in an attempt to reduce attraction by traps of *P. cygnus* from one reef to another.

During the initial tagging in January 1981, trapping was conducted on each reef for four consecutive days, while during each subsequent recapture

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Numbers of juvenile *Panulirus cygnus* examined on three reefs at Seven Mile Beach, Western Australia.

	Sampling dates							
Reef	1981	1981	1981	1981	1981	1981	1982	1982
	9–10 Jan.	6–7 Feb.	Mar.	May	26–27 Aug.	21–22 Sept.	26–27 Jan.	26–27 Feb.
Reef I								
No. caught	463	447	—	—	362	300	498	419
No. tagged	463	—	—	—	—	—	—	—
No. recaptured	—	103	—	—	98	72	88	[1]5
	11–15 Jan.	4–7 Feb.	10–11 Mar.	5 May	24–25 Aug.	19–20 Sept.	24–25 Jan.	23–25 Feb.
Reef III								
No. caught	1,202	785	475	233	221	359	791	862
No. tagged	304	—	—	—	—	—	—	—
No. removed from reef	898	306	150	—	—	—	—	—
No. recaptured	—	[2]+	+	54	52	55	204	[1]13
	11–15 Jan.	4–7 Feb.	10–11 Mar.	5 May	24–25 Aug.	19–20 Sept.	24–25 Jan.	23–25 Feb.
Reef V								
No. caught	141	682	596	424	599	631	703	696
No. tagged	1,141	—	—	—	—	—	—	—
No. recaptured	—	278	214	154	212	285	140	28

[1]Additional to those recaptured in January 1982.
[2]+ = not scored.

period trapping was conducted for two consecutive days. The single mark-recapture estimate of Bailey (1951) was used to calculate population sizes.

Visual Estimates of Population Size

Direct estimates of the total number of juveniles present on each test reef were made by two divers during the day. Initially the surface of each test reef was mapped, and the map was transferred to acetate writing sheets for use underwater, so that major features such as crevices, holes, and sections of ledges could be recognized and searched in a uniform manner during each census. The two divers moved slowly around and over the reef, counting and recording juvenile *P. cygnus*. Underwater lights were used to aid in this process. Repeated counts were often necessary to obtain consistent results for sections of the reef with large aggregations of juveniles. One diver followed approximately 2–3 m behind the other, and after each section of the reef was censused, the numbers of juvenile *P. cygnus* recorded by the two divers were compared. Only three observers conducted all of the visual censuses and, after experience was gained initially, differences between total counts by any two divers on a reef usually were less than 5%. Counts by the two divers were compared for 12 of these censuses, employing separate Wilcoxon signed-rank tests in which the data recorded by each diver for a given section of the reef were paired. The results for all 12 censuses indicated no significant differences in counts between divers ($P > 0.05$).

There are two primary sources of error in this method. One is that few individuals <40 mm CL can be seen on the surface of the reef or in holes or crevices. The other results from reduced visibility caused by turbidity and water turbulence. This second problem was largely avoided by only doing counts when conditions of turbidity and water turbulence were favorable.

During January–June 1981 and October 1981–February 1982, visual density estimates were obtained monthly or bimonthly in reefs III and V. However, storm conditions and poor visibility during the remainder of 1981 precluded observations. Visual density estimates were conducted on reef I during January 1981 and in January and February 1982, while in January and February 1983 estimates were conducted on all three test reefs.

Density Manipulation Experiment

All of the juvenile *P. cygnus* caught on reefs I and V (the control reefs) in January 1981 were tagged, measured, and released. On reef III (the treatment reef) 1,202 *P. cygnus* were caught during four consecutive days in January 1981 and graded into size categories (5 mm CL size intervals). This was done by measuring the animals and holding them in water in mesh bags suspended from the side of the boat during the 2–3 hours required for processing.

To reduce the population of lobsters on reef III by approximately 75%, three out of each four animals in each size group were removed from the reef and translocated to another locality out of the Seven Mile Beach area. Selection was done by removing the appropriate number of individuals from each size category blindly to avoid bias. This helped to assure that the groups of juveniles returned to reef III had a size frequency and sex ratio similar to those of the original population. The remaining 304 juveniles caught from reef III were remeasured, tagged, and released on that reef. During the next two sampling periods in February and March 1981, any untagged *P. cygnus* caught on reef III were removed (Table 1) to aid in maintaining the density at approximately 25% of its natural level.

Analysis of the Growth Data

Two types of growth data were examined: 1) the single molt increments of animals with <4 legs missing (based on the growth of animals recaptured within four months of a previous capture) (Chittleborough 1976), and 2) the average relative growth rate (Sandland and McGilchrist 1979), which has been shown to be appropriate for analyses of *P. cygnus* growth (Phillips et al. 1983). The data were classified by reef, sex, age class, duration, and time of year at liberty and by the number of legs missing at the time of tagging.

The average relative growth rate data of *P. cygnus* were condensed into a three-factor nonorthogonal experimental design with missing cells. The data were analyzed by examining differences in growth between test reefs for each age and recapture interval, using the Wilcoxon rank sum test, and by examining age, recapture interval effects, and their interaction in a two-factor nonorthogonal analysis of variance.

In addition to *P. cygnus* caught on the reef of original tagging, 75 individuals (12%) were recaptured on both reefs III and V. The data for the 49

of these which showed growth between tagging and recapture were initially analyzed separately.

Chittleborough (1970) found that loss of more than three legs depressed growth. This was confirmed for our data by an analysis comparing the average relative growth rates of *P. cygnus* in the two leg-loss classes (<3 legs missing and ⩾4 legs missing), using a *t*-test. There was a significant difference in growth rates between the two leg-loss classes ($P > 0.05$). Although this difference is confounded with differences in the other factors, the result was considered as sufficient evidence, when combined with Chittleborough's findings, to exclude from further analysis data for *P. cygnus* with ⩾4 legs missing.

A further analysis was performed to determine if the growth rates of males and females differed. These analyses were done separately for each reef, age class, and recapture interval, using the Wilcoxon rank sum test. The results revealed no significant differences in average relative growth rates between the sexes ($P > 0.05$), so the data for males and females of the same age group were pooled.

RESULTS

Of the 304 tagged *P. cygnus* on reef III, 186 (61.2%; 87 males and 99 females) were never recaptured, while of the 1,141 animals tagged on reef V, 636 (55.7%; 324 males and 312 females) were never recaptured. Similarly, of the 463 *P. cygnus* tagged in January 1981 on reef I, 307 (66.3%; 162 males and 145 females) were never recaptured. Comparison of the size ranges and size-frequency distributions of *P. cygnus* tagged on the three reefs in January 1981 with those not recaptured (Fig. 2) indicated that the "losses" were distributed equally over the full size range and therefore may be assumed to be random. Ratios of males and females in these "losses" did not differ significantly from the male:female ratios in the original tagged population (chi-square test of independence, $P > 0.05$).

None of the tagged *P. cygnus* on reef I were recaptured on reef III or V. However, 75 (12%) of the tagged *P. cygnus* either on reef III or V were subsequently recaptured on the other reef, and some were caught several times on reefs III and V. However, only four of the animals originally tagged on reef III were ever recaptured on reef V, suggesting a general movement of *P. cygnus* from reef V to reef III, i.e., inshore to offshore.

Size and Age Structure

The size-frequency distributions of *P. cygnus* juveniles on reef I in January 1981 and January 1982 and that of the juveniles recaptured in January 1982 are shown in Figure 3. Similarly, the size-frequency distributions of juveniles on reefs III and V in January, May, and September 1981 and in January 1982 are shown in Figure 4. There was change in the composition of the population on reef I between January 1981 and 1982, indicating immigration of 2- and 3-yr-old animals into the population of this reef. Between January and September 1981 there was an indication of immigration of untagged animals to both reefs III and V, principally of animals ⩾3 years of age, while in January 1982 there was also an obvious immigration of 2-yr-old animals to both reefs.

Population Size, Density, and Mortality Rates

The estimates of population size, density, and mortality rates for *P. cygnus* juveniles ⩾3 years of age on reefs I, III, and V are given in Table 2. The estimate made for the population on reef III in February 1981 assumes that the 304 tagged *P. cygnus* released in January were still within the population in February.

The population densities of ⩾3-yr-old juveniles on reef I estimated each January from 1970 to 1982 are shown in Figure 5. The density in January 1981, at the time the study began, was the highest ever recorded. The density in January 1982 was also very high and only exceeded by the levels in January 1974 and January 1981.

The annual mortality coefficient for juveniles aged

TABLE 2.—Population size, population density and mortality-rate estimates for juvenile *Panulirus cygnus* >3 years of age on three test reefs at Seven Mile Beach, Western Australia.

	[1]Reef 1 (0.071 ha)		[2]Reef III (0.104 ha)		[3]Reef V (0.103 ha)	
Date	Population	SD	Population	SD	Population	SD
Jan. 1981	1,990	170	2,192	194	2,644	120
Feb. 1981	—	—	1,879	195	—	—
Aug. 1981	625	38	725	54	1,042	40
Jan. 1982	1,273	93	1,951	92	1,841	101

[1]Annual instantaneous mortality coefficient for those >3 years in 1981 = 1.655.
[2]Annual instantaneous mortality coefficient for those >3 years in 1981 = 1.302.
[3]Annual instantaneous mortality coefficient for those >3 years in 1981 = 1.825.

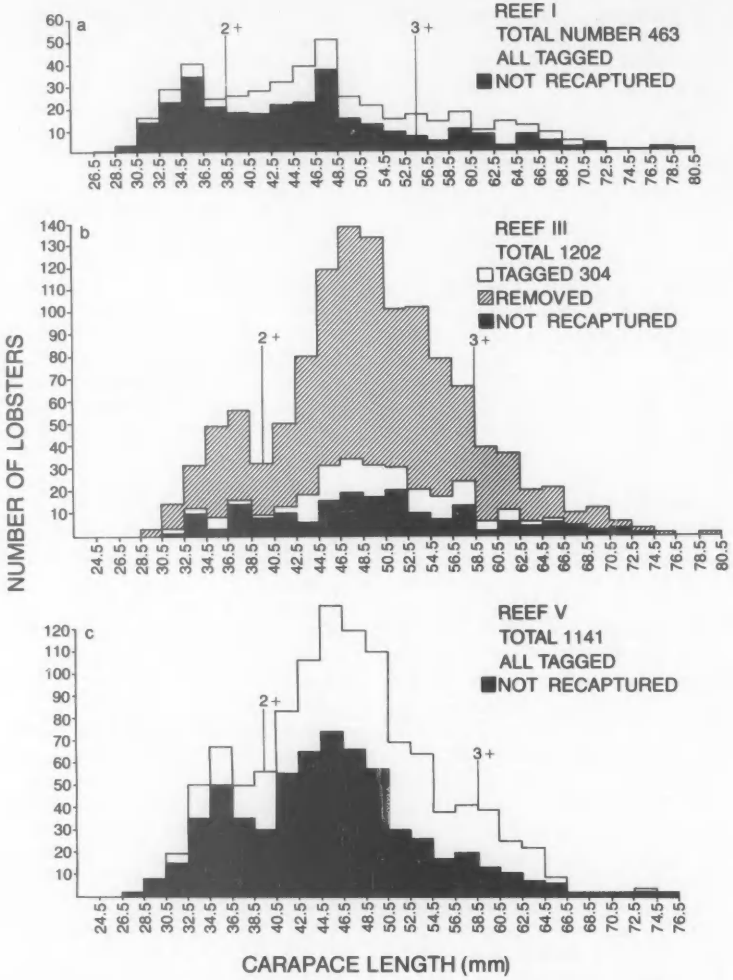

FIGURE 2.—Size-frequency distributions of juvenile *Panulirus cygnus* in January 1981 on three test reefs (reefs I, III, and V) at Seven Mile Beach, Western Australia and size-frequency distributions of animals removed or tagged. Size-frequency distributions of tagged animals not subsequently recaptured also are indicated.

≥3 years on reef III was slightly lower than that for juveniles on reefs I and V. Comparison of the estimates of population size on which these mortality coefficients were based showed that annual survival of animals ≥3 years old was significantly higher on reef III than on reef V (chi-square test of independence, $P < 0.005$).

The numbers of juveniles tagged and released on each test reef in January 1981 are shown in Table 1, while the numbers and percentages of those same individuals recaptured on the same reef in January or February 1982 are summarized in Table 3 for each age group. These data were used, in part, to provide more specific estimates of age-specific sur-

vivorship over the 1-yr period, based on assumptions considered later in this paper. A striking feature of the data for reef III is the very high percentage of recaptures, ranging from 97.4 to 100% for 3-, 4-, and ≥5-yr-old individuals, and with a somewhat lower value of 58.1% for 3-yr-old animals. Percentage recaptures for all age groups combined were 71.4% on reef III, as compared with much lower values on reef V (14.7%) and reef I (20.1%). Separate comparisons employing chi-square tests of independence indicated that the number of juveniles recaptured were significantly higher on reef III than on reef V for each of the four age groups ($P < 0.005$).

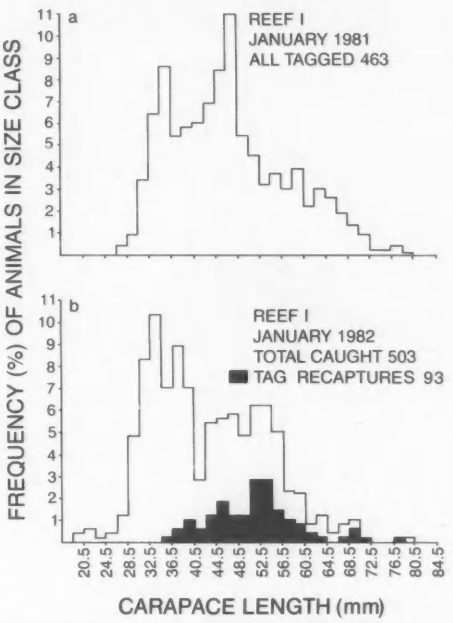

FIGURE 3.—Size-frequency distributions of juvenile *Panulirus cygnus* on Reef I at Seven Mile Beach, Western Australia, in January 1981 and 1983.

Visual Estimates of Population Size

Estimates of the mean total numbers of *P. cygnus* juveniles on the three test reefs, based on visual sampling by two divers, are summarized in Table 4.

The data for reef I are incomplete but show a dramatic decrease from 265 on 10 January 1981 to 66 on 19 January 1981. There was also an overall reduction from 265 in January 1981 to 181 in January 1982 and 173 in January 1983.

The data for reef III (Table 4) indicate that removal of *P. cygnus* by trapping on 11–15 January 1981 reduced the number of juveniles from 705 present on 10 January to about half of that number, with 395 (56%) observed on 19 January and 346 (49%) on 3 February. Further removal by trapping on 4 and 5 February 1981 reduced the number of juveniles to approximately 29% of the original 10 January level (205 observed on 18 February).

From March through June 1981 the mean estimated numbers of juveniles on reef III varied from 189 to 260, representing approximately 27–48 ($\bar{x}$ = 36%) of the original, natural population level observed on 10 January 1981 (Table 4). By January 1982, the number of juveniles on reef III had increased to 430, or approximately 61% of the level observed in January 1981 and by January 1983 the number had increased to 590 or approximately 84% of the natural level two years before.

The numbers of juveniles on reef V were rather more variable, ranging from a low of 72 (25 March 1981) to a high of 780 (October 1981). Of special im-

TABLE 3.—Number and percentage of juvenile *Panulirus cygnus* tagged in each age class on three reefs at Seven Mile Beach, Western Australia, in January 1981, and the numbers present and recaptured in January and February 1982.

	Reef I				Reef III				Reef V			
Age class (Yr)	1981 No. tagged	1982 Total no. caught	1981 Recaptures No.	%	1981 No. tagged	1982 Total no. caught	1981 Recaptures No.	%	1981 No. tagged	1982 Total no. caught	1981 Recaptures No.	%
2	117	260	12	10.3	38	227	37	97.4	192	338	12	6.3
3	245	196	62	24.4	203	375	118	58.1	777	267	102	13.1
4	77	36	14	18.2	57	109	56	98.2	149	112	45	30.2
≥5	15	6	5	33.3	6	92	6	100.0	23	14	9	39.1
Total	463	503	93	20.1	304	804	217	71.4	1,141	731	168	14.7

[1]In January 1981

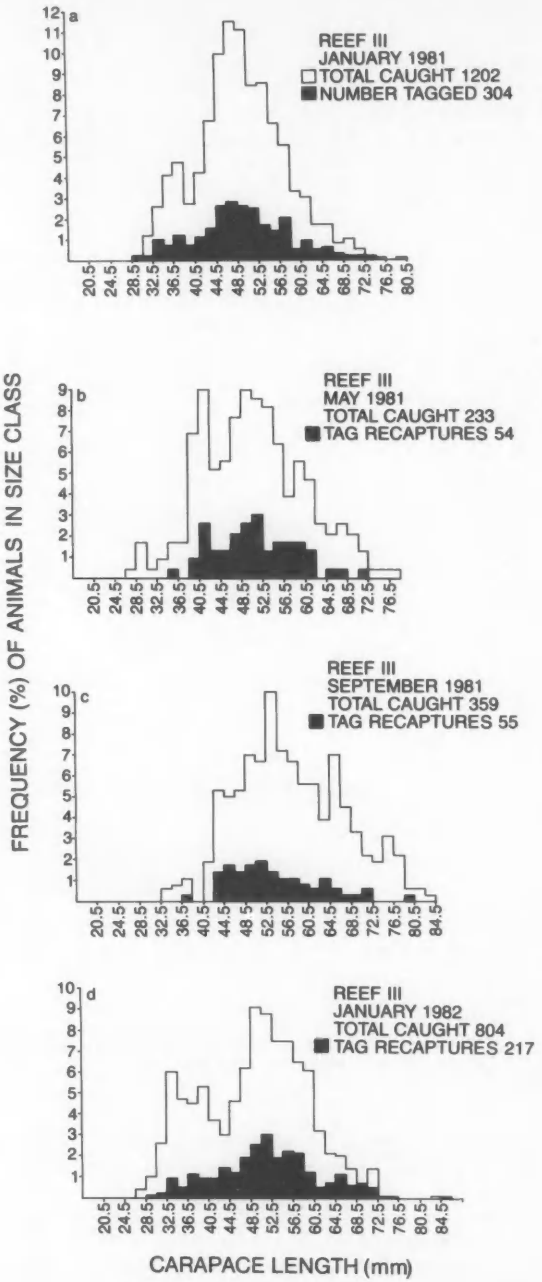

FIGURE 4.—Size-frequency distributions of juvenile *Panulirus cygnus* on reefs III and V at Seven Mile

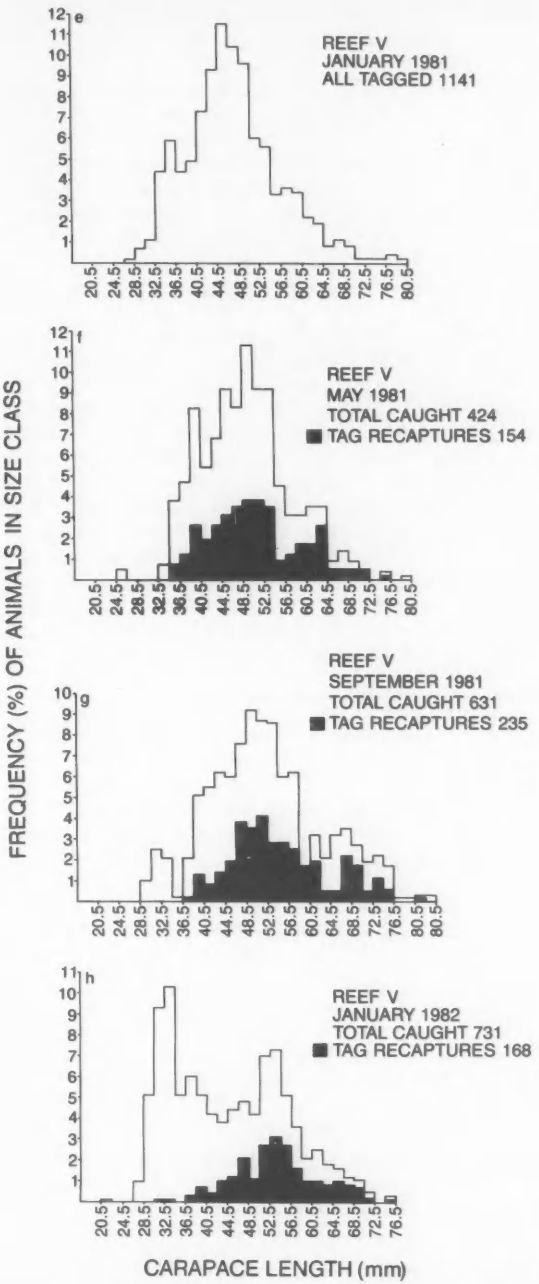

FIGURE 4.—*Continued*—Beach, Western Australia, during the period January 1981 through January 1982.

portance was the 34% decline in numbers between 10 January and 18 February on reef V. By mid-February 1981 the estimated population on reef V was below that on reef III. The mean number of animals for reef V in February 1982 (401) was 71% of that observed in January 1981 (563), although in October, November, and December 1981 it exceeded the January 1981 level. In January 1983, the number of juveniles (537) was essentially the same as that observed two years before (Table 4).

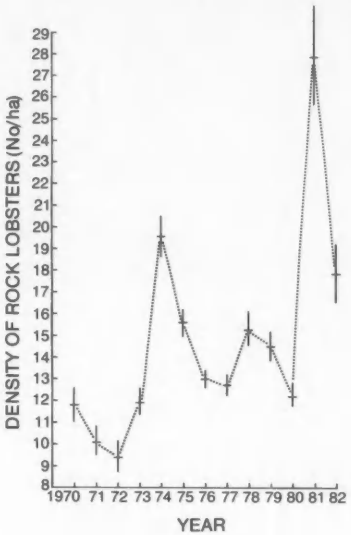

FIGURE 5.—Densities of 3-yr-old juvenile *Panulirus cygnus* in January on reef I at Seven Mile Beach, Western Australia, for the period 1970 through 1982. Mean and 95% confidence limits are shown. Data for 1970–80 from Morgan et al. (1982).

TABLE 4.—Mean total numbers of juvenile *Panulirus cygnus* on three test reefs at Seven Mile Beach, Western Australia, based on visual estimates made by two observers. — = no visual estimate made.

Date	Reef I	Reef III	Reef V
10 January 1981	265	705	563
19 January 1981	66	395	286
3 February 1981	—	346	235
18 February 1981	—	205	191
9, 13 March 1981	—	335	227
25 March 1981	—	189	72
23 April 1981	—	233	220
15, 17 June 1981	—	260	451
15 October 1981	—	374	780
19 November 1981	—	424	680
10 December 1981	—	321	647
29 January 1982	181	430	—
23 February 1982	42	474	401
11 January 1983	173	590	537
16 February 1983	121	521	501

Growth

Single Molt Increments

Mean single molt increments of male and female *P. cygnus* on reefs III and V, the treatment and control reefs, (Table 5) showed no significant difference within either the 2-, 3-, or 4-yr-old age-classes (t-test, $P > 0.05$). Only four animals estimated to be ≥5 years of age were recaptured and these were all from reef V. After pooling the molt increment data for the two sexes there were no significant differences between the mean single molt increments of 2-, 3-, or 4-yr-old animals on reefs III and V (t-test, $P > 0.05$).

TABLE 5.—Mean molt increments in carapace length (mm) for sex age-class groups of juvenile *Panulirus cygnus* from three test reefs at Seven Mile Beach, Western Australia during January–May 1981. Data are mean SE (*n*).

Age class	Reef I		Reef III		Reef V	
	Males	Females	Males	Females	Males	Females
2	—	—	2.58(0.40) (5)	1.84(0.11) (5)	1.75(0.28) (4)	2.41(0.20) (10)
3	2.85(0.56) (6)	1.74(0.21) (9)	2.01(0.33) (16)	1.76(0.15) (16)	2.27(0.14) (76)	2.17(0.26) (60)
4	—	—	2.75(0.61) (4)	1.94(0.26) (5)	3.17(0.26) (16)	2.88(0.19) (18)

The data from reef I, the secondary control reef, were only sufficient for an examination of the single molt increments of 3-yr-olds. Within this age class there was no significant difference in mean molt increment between the two sexes and the data for the whole age class were pooled. There were no significant differences between the mean single molt increment for 3-yr-olds from reef I and the mean single molt increment for this age class on either reefs III or V (t-test, $P > 0.05$).

Annual and Seasonal Growth

The mark-recapture data from reefs I, III, and V are considered within four time periods: From January 1981 to May 1981 (the "summer–autumn" period), from May 1981 to September 1981 (the "winter" period), from September 1981 to February 1982 (the "spring–summer" period) and from January 1981 to January–February 1982 (the "annual" growth period). As described in Methods section above, average relative growth rates (ARGRs) of males and females were not significantly different and therefore the data were pooled. Because of the small number of ≥5-yr-old lobsters, their growth data were combined with the data for the 4-yr-old individuals. The ARGRs of the different age groups from all three reefs over each of the four time periods are given in Figure 6.

Comparison of growth data for the test reefs for each age group and recapture interval were made using Wilcoxon rank sum tests. The primary purpose was to evaluate whether growth data for the three reefs could be pooled for later analysis. The comparisons are of interest in their own right, but caution is required in interpreting some of the differences established because of small sample sizes in some cells.

The results showed no significant differences in ARGRs of any age group between reefs III and V ($P > 0.05$), the treatment and the principal control reefs respectively in the density manipulation experiment. There were significant differences in ARGRs between reefs I and III for individuals 3 years of age in January–May 1981, May–September 1981, and January 1981–January 1982 and for individuals ≥4 years of age in January–May 1981. There also were significant differences in ARGRs between reefs I and V for individuals 3 years of age in January–May 1981 and May–September 1981, and for individuals ≥4 years of age in January–May 1981 ($P < 0.05$). The significant differences all showed consistently higher ARGRs on reef I than on reefs III and V.

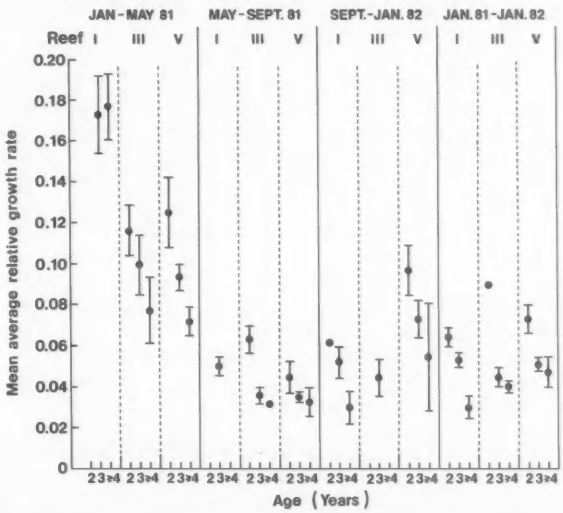

FIGURE 6.—Average relative growth rates (ARGRs) of juvenile *Panulirus cygnus* on test reefs at Seven Mile Beach, Western Australia.

The data for both reefs III and V were then pooled. The data for 49 *P. cygnus* which were recaptured on reefs III and V were included in this set (Fig. 7). Comparisons of these combined data were made with the data for reef I, and the results indicate that all of the significant differences in growth described above were maintained except that for 3-yr-old individuals in January 1981–January 1982. The lack of a consistent significant difference between reefs at all ages and recapture intervals suggests that the effect is not a simple response to a superior environment, but rather that interactions between reef and age and between reef and recapture interval are present.

DISCUSSION

The density manipulation described in this paper is an attempt to use an ecological field experiment in a nonbenign, subtidal habitat to study the population processes of a spiny lobster. Practical limitations within this environment related to wave effects on drifting plant material and the need to enclose enough area to adequately provide for the foraging range of juvenile *P. cygnus* precluded the use of large enclosures which would have effectively prevented migration. Also, because of the potential mobility of *P. cygnus*, it was not possible to increase and maintain the density of juveniles above natural levels on a reef without such an enclosure. Therefore, only an experimental reduction in density was attempted:

1. Data from the visual estimates show that we were successful in reducing the number of juvenile *P. cygnus* on reef III to approximately 30% of the original, natural level by removing animals in January, February, and March 1981. Following the last removal, the estimated numbers of animals varied, but showed a slow increase over the 1-yr period of the manipulation experiment, with a mean of 36% of the original January level during March through June 1981 and a mean of 55% of the original level during October 1981 through January 1982. However, the number of juveniles on both reefs I and V, the control reefs, also declined during this period, and the population on reef V was estimated to be below that of reef III on 18 February 1981. Therefore, it is difficult to separate the effects of the systematic removals from a general decline in numbers indicated by what was observed on reefs I and V.

   The size and age structures and the sex ratios of *P. cygnus* juveniles on reefs I, III, and V in January 1981 were very similar. Size and age structures and the sex ratios of these juveniles

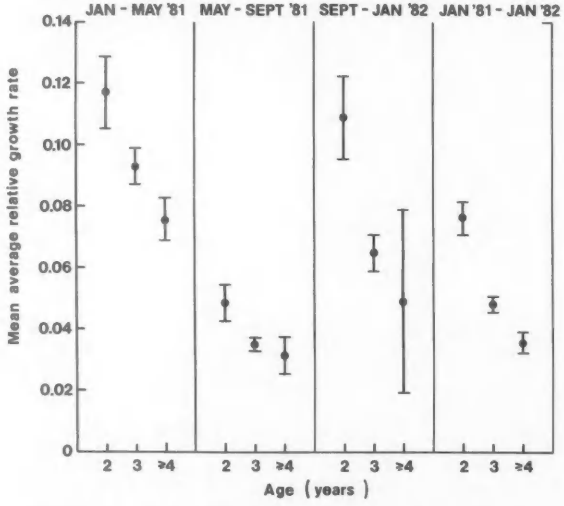

FIGURE 7.—Average relative growth rates (ARGRs) of juvenile *Panulirus cygnus* on test reefs III and V (combined) at Seven Mile Beach, Western Australia.

also were very similar among the reefs at all subsequent sampling times, suggesting that the drastic reduction in the density of *P. cygnus* on reef III, and the method of reconstituting the population, did not have an evident effect on these characteristics over the 1-yr period of the experiment.

2. The population sizes of ⩾3-yr-old *P. cygnus* juveniles, estimated from catches with baited traps, were significantly lower on reef III than on reef V in January 1981 and August 1981, but were similar (i.e., not significantly different) in January 1982. However, these data, and the estimates of mortality derived from them, are subject to the usual problems associated with mark-recapture techniques. Phillips (unpubl. data) has found in more recent studies that the baited traps are capable of attracting juveniles from over a wide area and hence the population size and density estimates applied to individual reefs probably are inaccurate. However, the trends in the population estimates from the mark-recapture data are supported by the visual estimates of population size, indicating that they reflect what was actually happening on these two reefs.
3. Clearly, the visual estimates provide a more specific set of information about population levels of juveniles living on the reef. The method also allows direct estimates of numbers over short time intervals and with minimal disturbance of the western rock lobsters. However, although there is no doubt about the drastic decline in the numbers of tagged lobsters on reefs I and V after the period of initial tagging, it is not possible to determine if this was as a result of tagging mortality, an emigration as a response to handling and tagging or part of the normal behavior pattern.

Despite the attempts to select directly comparable reefs for the experiment, it is possible that reefs III and V do provide different environments for the resident *P. cygnus*. The movement of 71 individuals from reef V to reef III may be part of a typical movement from shallower to deeper reefs. It seems unlikely that water depth, per se, is the primary factor involved, because the difference in depth between the two reefs is no more than 2 m. The reefs used by Chittleborough (1970) at Garden Island, on which he found *P. cygnus* juveniles remained for several years with little movement even from one part of the reef to another, were similar in depth to reef III.

Observations during sampling indicated that on reefs I and V, which are both located close to the beach, relatively large amounts of plant detritus build up around the base of the reef and under ledges and that turbidity of the water is sometimes quite high. These effects also occur on reef III, but are less pronounced. This suggests that less favorable conditions on the shallower, inshore patch-reefs may cause some *P. cygnus* to seek reefs slightly farther offshore which have more suitable conditions. It also may help to explain the higher variability in numbers of juveniles from the visual estimates made on reef V compared with reef III. Some individuals may temporarily emigrate from areas such as reef V during periods of adverse conditions.

Survival and mortality data, which were obtained from both the mark-recapture estimates of population size and the numbers of tagged animals recaptured on the same reef, indicate that survival of *P. cygnus* juveniles was significantly higher on reef III than on reef V over the 1-yr period of the experiment. This was evident for individuals of all four age groups. It suggests that the experimental reduction in numbers of juveniles on reef III, resulting in relatively low population densities (29–61% of the original, natural number) during the 1-yr experimental period, led to significantly higher survival than on reef V, where *P. cygnus* juveniles were present at natural density levels. One explanation for this is that reduced densities of juveniles on a reef may lead to a corresponding reduction in predation mortality and adverse interspecific effects of crowding. An alternative explanation for the very high survival of *P. cygnus* juveniles estimated on reef III, relative to reefs I and V, is that the tagged juveniles on reef III remained for the entire year while many of those tagged on reef I and V emigrated to other reefs.

These mortality data are subject to several sources of error, including the basic problems associated with mark-recapture sampling to obtain population estimates (Bailey 1951). The age-specific estimates of survival obtained from comparisons of numbers of tagged individuals released on each reef in January 1981 and recaptured there in January or February 1982 requires a major assumption. It is that all of the tagged individuals not recaptured on a particular reef after one year have died. This undoubtedly is not the case because some of those individuals probably moved to other reefs at Seven Mile Beach after their release. To the extent that this occurred, the survivorship estimates are low.

No quantitative information is available to correct the estimates for this effect.

The analyses of the growth data, including both the single molt increments and the ARGRs, clearly indicated high variability in growth rates between age groups, and that site (reef) and season variations (recapture interval) were compounding factors. Estimates of growth made during the 1-yr period of the study were similar to those obtained on reef I in previous studies at Seven Mile Beach (Chittleborough 1970, 1975, 1976; Chittleborough and Phillips 1975; Joll and Phillips 1984). However, despite the fact that the population densities in 1981 were the highest ever recorded, the molt increments of the 3-yr-old *P. cygnus* were significantly higher than at the low densities in 1971–74.

Comparisons of the growth data for *P. cygnus* juveniles showed no significant differences in growth within any age group between reefs I, III, and V. The reduced densities of juveniles on reef III had no apparent effect on either their overall growth rates or their molt increments. This suggests that the food resources on the surrounding seagrass beds may not limit growth within the range of *P. cygnus* densities present on these reefs during the field experiments. However, other factors may be involved. The foraging ranges of juveniles on reef III may overlap those animals from reef V and other nearby patch-reefs. More recent acoustic tracking studies by Jernakoff (unpubl. data) suggest that this is probably the case. If so, then reducing the density of *P. cygnus* on reef III might not produce a significant increase in their growth rates, because they could still be sharing their food resources with animals from nearby reefs.

The best tests of hypotheses about the effects of limited resources are those where the densities of *P. cygnus* are experimentally manipulated in replicated experimental areas and which incorporate appropriate controls (Connell 1974; Underwood 1979). This attempt has highlighted a number of problems. Nevertheless, it may be useful to conduct modified manipulation experiments of this kind in the future. Obviously, one of the problems with the present experiment was the lack of replication, and replication should be incorporated in the design of any future experiments. This was not possible in the present study because of high time and manpower requirements associated with the use of trapping and mark-recapture techniques. Furthermore, our observations indicate that it will be extremely difficult to find a series of patch-reefs similar enough in size, structure, and other features to serve as true replicates. As has been shown in this study, even small differences in water depth, or as yet unidentified characteristics, make the selection of reefs as equivalents very difficult. Selection of such reefs also will not be easy because often several reefs are within the known foraging range of the juveniles.

Evaluation and refinement of the visual estimation technique also will be necessary before further manipulation experiments are undertaken, as the usefulness of mark-recapture techniques is dubious. Without the development of such a refined method which would permit rapid and frequent estimates of population size, the effect of subsequent changes in population levels cannot be properly monitored. Without such a method it also would not be possible to determine the extent to which migrations of *P. cygnus* juveniles to and from the reefs are induced by the use of the baited traps or by handling and other disturbances during the mark-recapture process.

ACKNOWLEDGMENTS

We thank David Wright, David Evans, Simon Braine, and Leo Olsen of the CSIRO Division of Fisheries Research, Marmion, Western Australia, for their assistance with field and laboratory work. We also thank Frank W. Reneke of San Diego State University and R. Sandland of the CSIRO Division of Mathematics and Statistics for their assistance with computer data summaries and statistical analyses. This study was sponsored by the National Science Foundation U.S.-Australia Cooperative Science Program through NSF grant INT 7927203 to Richard F. Ford and by the CSIRO Division of Fisheries Research.

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A LONG-TERM STUDY ON THE BEHAVIOR AND SURVIVAL OF EARLY JUVENILE AMERICAN LOBSTER, *HOMARUS AMERICANUS*, IN THREE NATURALISTIC SUBSTRATES: EELGRASS, MUD, AND ROCKS

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ABSTRACT

An 8-month study on the behavior, growth, and survival of early juvenile American lobsters, *Homarus americanus*, was conducted in three different naturalistic habitats of mud, rocks with algae, and eelgrass. Fifteen narrow aquaria (10 cm wide) allowed visual observations of American lobster's activities in five replicates of each of the three habitats. After a 3-month acclimation period to establish "natural" benthic communities which entered through the water supply, three stage IV American lobsters were introduced into each aquarium. Observations were made on the settling, burrowing, activity, and feeding behavior of these lobsters.

American lobsters in eelgrass and rock habitats settled into the substrate more quickly, had burrows a greater percent of the time, and spent less time repairing their burrows than lobsters in mud habitats. The lobsters in eelgrass had a lower mortality rate than lobsters in either rocks or mud. None of the lobsters in any substrate were observed foraging for food outside of their burrows. However, the behavior of these American lobsters indicated that they were able to capture plankton drawn into their burrows by pleopod fanning. Six lobsters molted during the coldest part of the year when the water temperature was approximately 1° to 2°C.

Stage IV of the American lobster, *Homarus americanus*, is best described as transitional between larval and juvenile (Phillips et al. 1980). During this stage major behavioral changes take place, which coincide with the morphological changes occurring in the molt. These behavioral and morphological changes cause the stage IV lobsters to descend from the upper layers of the water column to the bottom where they build a burrow (Botero and Atema 1982; Ennis 1975).

Knowledge of the American lobster's behavior from the onset of settlement until they reach a size of approximately 20 mm in carapace length (CL) remains limited because juveniles of this size range have been found in the field only sporadically.

Several laboratory experiments sought to determine the substrate preferences of stage IV American lobsters. Howard and Bennett (1979) found that lobsters (*H. gammarus*) generally choose the largest size of gravel provided (approximately 20 mm in diameter), because larger rocks have more available space between them for burrows. If given a choice between a gravel substrate or a silt/clay substrate, American lobsters prefer the gravel (Pottle and Elner 1982). In choice tests, stage IV American lobsters preferred rocks with macroalgae, followed by, in order of decreasing preference, mud, rocks on sand, and sand. If not afforded a choice, the lobsters settled most quickly on the rocks with macroalgae, followed by rocks on sand, mud, and sand (Botero and Atema 1982).

MacKay (1926) recorded observations on the lobsters' ability to burrow in mud. Subsequently Cobb (1971), Berrill and Stewart (1973), and Botero and Atema (1982) have described the methods by which juvenile American lobsters make burrows in both mud and rocky substrates. No observations have been made on American lobsters burrowing into other substrates, such as eelgrass or peat.

Cobb et al. (1983) followed stage IV *H. americanus* for short periods of time following their release into the field. They observed behavior which may indicate that American lobsters test different substrates and continue moving if they are on unsatisfactory substrates such as sand or mud; however, only two lobsters were actually seen rejecting a substrate.

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Manuscript accepted July 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

None of the previous studies lasted for more than a few days, and long-term behavioral observations have never been recorded on early juvenile American lobsters. There are virtually no field data on simple life history parameters such as their preferred substrate, growth rate, diet, and behavior. It is unwise to proceed with experimental laboratory studies on an organism without having a descriptive life history background to provide context. Both Cobb (1987) and Fogarty (1987) recognized the need for more studies on the behavior and ecology of the postsettled prerecruits used in this study. At present it is difficult to gather such information in the field. However, this study was designed in order to provide such a background by carefully creating naturalistic habitats in the laboratory. We present quantified behavioral observations, survival, and growth of early juvenile American lobsters in three different substrates: mud, rocks, and eelgrass, over an 8-mo period.

MATERIALS AND METHODS

Fifteen "ant farm" aquaria (45 cm deep × 30 cm long × 10 cm wide) were constructed to optimize our ability to observe the American lobsters inside their burrows. Five of the aquaria were two-thirds filled with cohesive mud (particle size <0.06 mm) collected from mud flats in the Woods Hole, MA area. Five of the aquaria were two-thirds filled with rocks, collected from subtidal areas in such a way that a representative distribution of rock sizes was obtained (0.1–20 mm diameter). Some of the rocks in each tank had macroalgae *Coleus* (sp.) and *Fucus* (sp.), or both growing on them. Eelgrass collected from local eelgrass beds was placed in the last five aquaria; less substrate was used in these latter tanks so that the eelgrass leaves had room to grow.

The aquaria were randomly distributed in a system which provided running, unfiltered seawater at ambient temperatures seasonally ranging from 23° to 0°C. Plankton were always visible; also the three habitats occasionally had plankton blooms, during which algae and zooplankton were plentiful. The tanks were maintained on an ambient light/dark regime with a light intense enough to keep the eelgrass alive. Removable, opaque, black plastic was placed around each aquarium to the level of the substrate to ensure that the lobster burrows were dark. To establish "natural" benthic communities, the tanks acclimated from 20 July until 16 October 1982, before beginning the experiment.

Stage IV American lobster siblings from the hatchery at St. Andrews, New Brunswick, Canada were introduced, one per day into each aquarium for 3 consecutive days. Thus, the total number of lobsters at the start of the experiment was 45, 15 per treatment. Observations were recorded continuously for the first half hour after each introduction and then for the following 1.5 hours; observations were recorded by scanning (taking an instantanious reading of the lobsters' behavior) every 10 minutes. Observations were made of the following: 1) location of the animal in the aquarium, 2) motion (walking, swimming, or resting), 3) burrowing activity (pleopod fanning, bulldozing, or digging), and 4) shape, size, and location of final burrow. This procedure was similar to that used in the substrate choice tests done by Atema et al. (1982).

During the first introduction of American lobsters into several of the tanks, mud crabs, *Neopanope sayi*, immediately consumed them. The mud crabs were subsequently removed and new American lobsters were placed into these tanks.

After the American lobsters had been introduced into each of the 15 tanks, long-term observations began of each lobster in each tank at intervals ranging from daily to twice per week. The observation periods were at different times during the day with 5.1% during the dark period, although it was difficult to see the lobsters in low light because of the cryptic nature of some burrows. There was a total of 195 observations periods. Each lobster that was visible was watched for at least one minute; if the lobster was active, observations lasted until the activity ended. However, for the quantitative analysis of lobster activity only the first minute of observations were used. A total of 495 hours of observations were made averaging 11 hours per individual lobster. For each lobster we recorded 1) the location of the lobster in relation to its burrow, 2) whether the lobster had molted, 3) the lobster's activity, and 4) the shape of the burrow (with a quick sketch). The activities observed are described in Table 1.

The experiment lasted approximately eight months, from 21 October 1983 to 1 July 1984. The lobsters were not fed during that time; we assumed they would find food from the communities in which they lived. At the end of the experiment, the surviving lobsters were weighed and their carapace length was measured. Additionally, the sediment in each tank was sieved through a 1 mm screen, and all organisms were collected, weighed, and identified to the genus or species level.

TABLE 1.—Description of the different activities observed throughout the experiment.

Activity	Description
Rest	No movement for at least 30 seconds. Grooming was not considered movement, and was not recorded separately from rest.
Pleopod fan (PPF)	Movement of the pleopods; if the fanning was being used to repair the burrows, i.e., sediment was being moved, then the activity was recorded as burrow repair.
Burrow repair (BR)	Any activity which caused sediment to be moved, including bulldozing (pushing sediment foward with the claws spread apart), pleopod fanning, and digging (loosening sediment by pushing claws into it).
Investigate (INVEST)	Standing at the entrance of the burrow with antennules out and antennae flicking.
Feed	Eating anything larger than 1 mm. Activity that looked like filter feeding was not included in this category (it was part of the pleopod fan). It is discussed in the text.
Walk	Walking on the sediment. Does not include "walking" in the burrow.
Swim	Swimming in the water column.

RESULTS

Burrowing

The American lobsters in the eelgrass and rock substrates started burrow construction more quickly than the ones in the mud substrate (1 way ANOVA, Newman-Keuls test, $P < 0.05$). There was no significant difference in the time to initial burrowing between lobsters in eelgrass and lobsters in rock substrates (Table 2A).

American lobsters used the same methods to make burrows in eelgrass as in mud and rocks. They typically started at the base of an eelgrass plant and then established a burrow under the rhizomes by pleopod fanning and bulldozing. The burrows usually had two openings although burrows were seen with from one to six openings. These openings were smaller and more difficult to see than similar openings in mud or rock substrates. Although lobsters in all substrates had burrows for the majority of the observations, because their burrow had collapsed, the lobsters in the mud substrate were without a burrow for a greater percent of the observations than the lobsters in the eelgrass or rock substrates (arcsine transformation, 1 way ANOVA, Newman-Keuls test, $P < 0.05$, Table 2B). For this analysis the lobster had to be visible; if neither the lobster nor its burrow were visible during a given observation period, that observation was excluded from the analysis.

Activity

American lobsters were not seen to forage outside of their burrows. If a lobster had a burrow, it was never seen outside of that burrow in any of the treatments during the entire experiment. During the day periods, these lobsters were seen in their burrows 1,503 times, and outside of their burrows 0 times. Therefore, by using sampling theory, one can calculate that the lobsters were spending at least 99.8% of their time during light periods in their burrows (binomial distribution, $P = 0.05$). During the night periods lobsters were seen in their burrows 103 times, outside of their burrows 0 times. Therefore, the lobsters were spending at least 97.0% of the time in their burrows during the dark (binomial distribution, $P = 0.05$). The difference between the night and day percentages is a function only of the greater number of observations made during the day.

The cumulative times that the American lobsters spent at various activities were influenced by sub-

TABLE 2.—(A) The average time in minutes that it took each lobster in the eelgrass, rock, and mud treatments to start construction of their burrow (eelgrass vs. mud and rocks vs. mud, $P < 0.05$). (B) The percent of observations throughout the experiment during which the lobsters in each substrate did not have a burrow. N varied from 160 to 68, depending on how many lobsters were visible (eelgrass vs. mud and rocks vs. mud, $P < 0.05$). (C) The average weight, in grams, and the carapace length (CL), in mm, of the lobsters in each treatment at the end of the experiment.

	A	B	C	
	Time to burrow	No burrow	Weight	and CL
Eelgrass	7.92 ± 2.02	4.70 ± 1.7	4.95 ± 0.95	18.15 ± 1.25
Rock	11.92 ± 3.22	3.82 ± 1.22	3.18 ± 0.16	15.22 ± 1.34
Mud	49.17 ± 14.08	12.2 ± 3.7	3.22 ± 1.23	15.85 ± 1.92

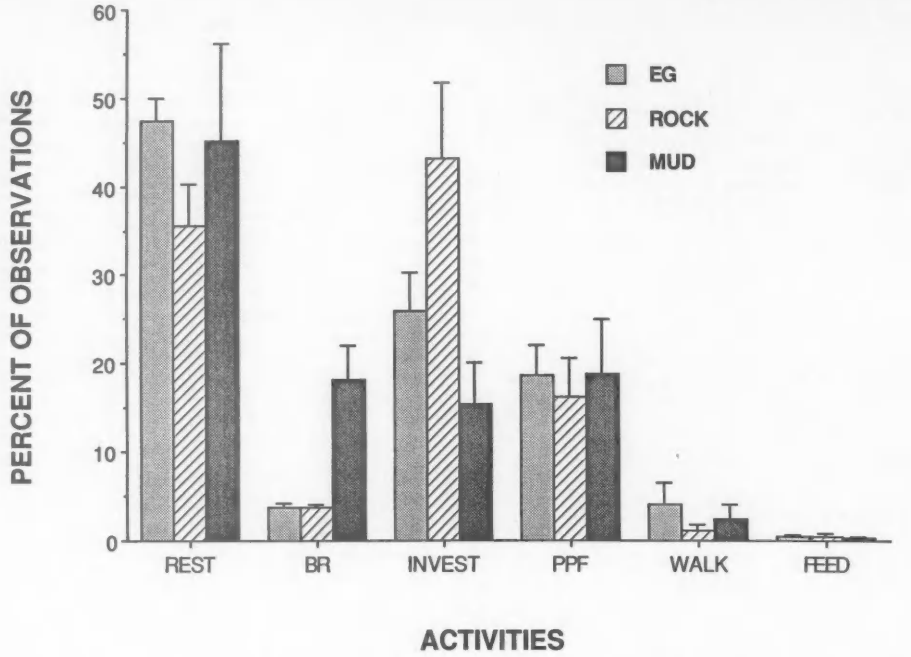

FIGURE 1.—The percent of observations in which the American lobsters were engaged in each of the listed activities. BR: eelgrass vs. mud, $P < 0.001$. Invest: eelgrass vs. mud and rock vs. mud, $P < 0.05$. N varied from 160 to 68.

strate (Fig. 1). The lobsters in the mud substrate spent a significantly greater percent of their time repairing their burrows than the lobsters in either eelgrass or rocks (arcsine transformation, 1 way ANOVA, Newman-Keuls test, $P < 0.001$). Based on percent of observations, the lobsters in mud spent significantly less time investigating than did the lobsters in rocks (tests as above, $P < 0.05$). There was no significant difference, however, between the percent of observations spent investigating in the mud vs. the eelgrass, or in the percent of observations spent investigating in the eelgrass vs. the rocks.

Based on the percent of observations, the time the lobsters spent resting and pleopod-fanning was considerable (18–45%) in all substrates and did not differ between them. Walking was only observed when a lobster did not have a burrow. Feeding occurred only on the few occasions when some edible object landed close enough to the burrow so that the lobster could reach it without entirely leaving its burrow. Twice lobsters were seen catching swimming amphipods at the entrance to their burrow.

American lobsters were observed creating a current by pleopod-fanning, which was seen to draw plankton through their burrows. During these periods the lobster stood with its clawed limbs held up and apart. The mouth parts, particularly the second and third maxillipeds moved rapidly, and the first pair of walking legs were often brought up to the mouth. Occasionally the lobster would jerk forward and snap its claws. All of the above-mentioned appendages are covered with various types of setae (Factor 1978), which could help the lobsters to catch the plankton both by "filtering" with their maxillipeds, claws, and first walking legs, and by seizing the plankton with their claws. These observations, supported by Lavalli and Barshaw (1986) and Barshaw (in press) show that American lobsters are able to catch plankton while remaining in their burrow.

Mortality

There was an initial mortality of the American lobsters in all habitats followed by no deaths in the winter and another die-off in the spring (Fig. 2). The mortality rate for American lobsters in eelgrass was significantly lower than those in the mud or in the rocks (arcsine transformation, linear, least-square regression, r^2 = 0.75 eelgrass, 0.86 rock, 0.94 mud, comparison of slopes, $P < 0.001$).

Molting and Size

At the end of the experiment there was no significant difference in the size of the lobsters between habitats, although the American lobsters in eelgrass tended to be larger (Table 2C). There was also no significant difference in the number of observed molts between treatments. We observed molting by six lobsters during the coldest part of the year when the water temperature was between 1° and 2°C.

Possible Prey

The biomass of American lobsters (>1 mm) was not significantly different among treatments, but the biomass of American lobsters in eelgrass tended to be higher (ANOVA, Newman-Keuls test, $P < 0.01$, Table 3). There were fewer different genera residing in the mud habitats, with the greatest diversity in rock.

DISCUSSION

Initial observations showed that stage IV American lobsters started to burrow more quickly in eelgrass and rock habitats. While several investigators have shown that American lobsters choose rocks over mud (Howard and Bennett 1979; Pottle and Elner 1982; Botero andAtema 1982), no choice experiments have used eelgrass as a substrate. Likewise, in this experiment we have not directly shown that the lobsters prefer the eelgrass substrate because they were not offered a choice. Speed of settling would be indicative of a preference, however, if the method that lobsters use to choose a substrate is to keep swimming if the habitat is unsuitable, but settle if it is suitable. Such behavior was observed in laboratory experiments by Botero and Atema (1982). Indications that lobsters keep swimming over unsuitable substrates was also observed by Cobb et al. (1983) in the field.

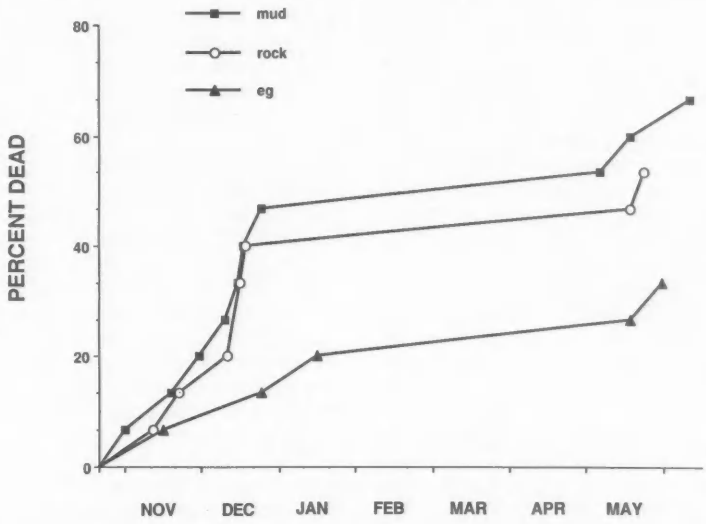

FIGURE 2.—The cumulative percent of American lobsters that died in the three treatments, each point represents a day when a lobster died. Fifteen lobsters per treatment were present at the beginning of the experiment. Eelgrass vs. mud and eelgrass vs. rock, $P < 0.001$.

TABLE 3.—Average biomass (wet weight) and species list of organisms larger than 1 mm living in the sediment of each treatment at the end of the experiment.

Treatment	Bivalve	Polycheate	Other
Eelgrass:	Mean biomass per tank = 8.2 ± 2.7 g		
	Mercenaria mercenaria	*Capitella* (spp.)	Sipunculoidea
	Yoldia (spp.)	*Clemenalla* (spp.)	(*Golfingia gouldi*)
		Glycera (spp.)	
		Lumbrineris (spp.)	
		Neris (spp.)	
		Spiondae (gen.)	
		Terebellida (gen.)	
Rock:	Mean biomass per tank = 3.28 ± 1.07 g		
	Andora ovalis	Chrysopetalidae	
	Andora transversa	(*Dysponetus pygmaeus*)	Sipuculoidea
	Mercenaria mercenaria	*Nephytidae* (spp.)	(*Golfingia gouldi*)
	Mucoma (spp.)	*Nereis* (spp.)	Crustacea
	Yoldia (spp.)	*Phyllodocdae* (gen.)	(*Neopanope sayi*)
		Sapella (gen.)	
		Terebellida (gen.)	
Mud:	Mean biomass per tank = 4.4 ± 1.07 g		
	Geukendia demessus	*Glycera* (spp.)	
	Solemya velum	*Nephtys* (spp.)	
	Yoldia (spp.)	*Nereis* (spp.)	
		Orbiniidae (spp.)	
		Terebelleda (gen.)	

The mud substrate appeared to be the least suitable of the three tested since American lobsters in eelgrass and rocks were without burrows for less time than those in mud. However, even in the mud habitat the lobsters had burrows for an average of 87.8% of the observations (Table 2B). The three substrates used in this study were chosen partly because of their differences, yet the lobsters managed to build and maintain burrows in all three substrates for eight months. This result clearly shows that early juveniles have flexible behavior and modify it to adapt to different substrates.

The way that the American lobsters partitioned the amount of time they spent on different activities was also affected by the substrate in which they lived. While lobsters in eelgrass and rock habitats spent little time repairing their burrows, lobsters in mud spent considerable time on repair (Fig. 1). This result is consistent with the characteristics of the three substrates. Eelgrass stabilizes the underlying sediment (decreases erosion) by baffling the water currents with its leaves and binding the sediment with its roots (Scoffin 1970); rocks, although usually found in areas of stronger currents, provide a ready made solid roof; mud, however, is more easily disturbed (Rhoads and Young 1970). If one lobster did not have a burrow in the mud tanks, its walking often destroyed the other lobsters' burrows.

The extra time that the American lobsters in mud spent repairing their burrows was subtracted mainly from investigation time (Fig. 1), perhaps because there was not as much prey in the mud for the lobsters to detect, so this activity was the most expendable. No significant differences were found between the time budgets of the lobsters in eelgrass and the lobsters in rocks; however, the lobsters in eelgrass spent more time resting than investigating, while the opposite was true of the lobsters in rock substrate.

The American lobsters in the eelgrass had a lower mortality rate than those in either mud or rocks. This result could have been due to the greater biomass of possible prey animals living in the eelgrass habitat, and/or the greater complexity of the eelgrass habitat, which in essence separated the lobsters and ameliorated the effects of high density. Seagrass beds in nature have also been shown to have a greater biomass of species living in them than the biomass of species living in less complex substrates such as mud or sand (Orth 1973; Thayer et al. 1984).

The lower mortality rate of lobsters in eelgrass led to a greater number of lobsters per tank in this treatment. Higher concentrations of lobsters have been shown to cause slower rates of growth in lobster living in fairly unnatural substrates (Cobb and Tamm 1974). In this study, the American

lobsters in eelgrass were not smaller perhaps also because the eelgrass substrate ameliorated the effects of higher density. We did not observe any differences in the activity budgets of the lobsters owing to higher density (Fig. 1).

This study shows that early juvenile American lobsters differ dramatically in their behavior from older lobsters. They seldom, if ever, forage for food outside of their burrows, but instead remain inside of them. This was true even though there were no predators present other than other juveniles.

The lobsters' main activities within their burrows reflected their needs. Because they did not forage outside of their burrows, all of the early juveniles' nourishment must have been found inside of their burrow, or within reach of the entrance. Lobsters could forage on polycheates, meiofauna, and on any other organisms residing inside their burrows or draw plankton in by pleopod-fanning. In this study lobsters were seen to catch swimming amphipods at the entrance to their burrow, and Berrill (1974) observed similar behavior. Besides resting, the lobsters mainly "investigated" for anything edible in the entrance of their burrow and pleopod-fanned to draw in plankton. If they were forced to burrow in a relatively unstable substrate, such as mud, they spent a significant amount of time maintaining that burrow.

The claws of early juvenile American lobsters are smaller and weigh less relative to the abdomen than those of older lobsters, and, by external appearance the two claws are not differentiated from each other. Furthermore, the speed of the tail flip reflex is faster at sizes smaller than 20 mm carapace length (Lang et al. 1977). These morphological characteristics along with the behavioral results from this study, and field observations that juveniles become easier to find at a carapace length of 20–40 mm (Cooper and Uzmann 1980; Able et al. in press), indicate that the juvenile stage of the American lobster can actually be divided into two substages: 1) the early juvenile stage, spanning settlement to the time until claws begin to differentiate, during which period the lobsters seldom, if ever, leave their burrow; and 2) the late juvenile stage, starting when the claws are differentiated and become larger in relation to the abdomen and ending with sexual maturity. At this stage, the lobsters start to forage for food outside of their burrows, and behave more similarly to adults (Cooper and Uzmann 1980; Able et al. 1988).

We suggest the following scenario for the life history of early juvenile American lobsters. After settling onto a suitable substrate the lobsters build a burrow where they remain for the duration of the "early juvenile" substage. By catching food, both in the substrate around their burrow entrance and by drawing plankton into their burrow by pleopod-fanning, the early juvenile lobsters manage to survive without foraging outside their burrow.

ACKNOWLEDGMENTS

We thank Diane Cowan and Ruth Iannazzi for help with observations and maintenance of the system. We also thank Mike Eagles then of the St. Andrews Marine Biological Field Station, New Brunswick, Canada for supplying us with stage IV American lobsters. We also thank Kenneth W. Able for reviewing the manuscript and Judith Capuzzo and Stanley Cobb for reviewing an earlier draft. This research was supported in part by a National Wildlife Federation - American Petroleum Institute, Environmental Conservation Fellowship to Diana Barshaw.

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DISTRIBUTION AND ABUNDANCE OF THE BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS* (MONTAGU, 1821), IN VIRGINIA[1]

ROBERT A. BLAYLOCK[2]

ABSTRACT

The distribution and abundance of the bottlenose dolphin, *Tursiops truncatus*, was examined by conducting aerial surveys of the Chesapeake Bay mouth and nearshore coastal waters of Virginia in 1980 and 1981. Bottlenose dolphin density was estimated using line transect methods and a 4-term Hermite polynomial was chosen to model the detection function. Six surveys in the Chesapeake Bay mouth resulted in an average density estimate of 0.159 dolphins/km^2. Ten surveys along the southern Virginia coast produced an average density estimate of 3.446 bottlenose dolphins/km^2 within 2 km of shore. Average bottlenose dolphin abundance in the Chesapeake Bay mouth and along the southern Virginia coast was estimated at 340 dolphins ($\pm$104, 95% C.I.). An estimate of 0.208 bottlenose dolphins/km^2 along the northern Virginia coast is tenuous because only one survey was conducted there. Dolphin sightings were distributed uniformly along the southern Virginia coast with the exception of some clustering of herd sightings at the capes bordering the Chesapeake Bay mouth. The percentage of calves per herd averaged 7.5% in Chesapeake Bay mouth, 4.3% in the southern coastal area, 9.0% in the northern coastal area, and peaked in June. Five of seven bottlenose dolphins identified by unique dorsal fin shapes in 1980 were resighted in 1981, suggesting seasonal residency of individuals.

Of the 23 cetacean species occurring along the Virginia coast (Leatherwood et al. 1976; Blaylock 1985) the bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), is the only cetacean found near shore regularly and in large numbers. However, there are few quantitative data available to assess the abundance, distribution, and seasonal occurrence of *Tursiops truncatus* (hereafter referred as *Tursiops*) in Virginia coastal waters.

Those bottlenose dolphins occurring seasonally in Virginia are believed to form part of a population distributed from northern North Carolina to New Jersey during the summer. This population was the focus of a sporadic fishery along Hatteras Island, NC from circa 1797 to 1929, the primary products of the fishery being hides and oil (True 1891; Townsend 1914; Mead 1975). From cumulative catch records, Mitchell (1975) estimated a historical population size of 13,748–17,000 dolphins and inferred annual migration from biannual peaks in catches during the fall and spring. True (1891) earlier suggested a north-south migration, reporting on fishermen's observations that bottlenose dolphins were usually seen traveling south in the fall and north in the spring, with only a few remaining near Hatteras during the summer.

Analysis of large-scale aerial surveys along the northern and mid-Atlantic U.S. coast revealed a bimodal longitudinal *Tursiops* distribution, interpreted as separate nearshore and offshore areas of abundance (CETAP 1982). These areas represent the habitats of two distinct morphological types of *T. truncatus*. The offshore type is slightly larger at the onset of physical and sexual maturity than the nearshore types and ultimately attains a greater size[3].

An important finding of the CETAP surveys was the presence of multiple latitudinal peaks in coastal sightings indicating discontinuities in the north-south distribution of nearshore *Tursiops* (CETAP 1982). These observations indicate either an uneven distribution of nearshore *Tursiops* or the presence of multiple coastal populations or subpopulations. However, a recent epidemic suggests that the U.S. east coast *Tursiops* may represent a single stock.

Tursiops mortalities south of North Carolina during autumn of 1987 increased sharply with the apparent emigration of *Tursiops* from Virginia

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Manuscript accepted June 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

waters.[4] If the high level of *Tursiops* mortalities experienced in the mid-Atlantic coast during the summer of 1987 was because of an infectious agent, then its spread to conspecifics in more southerly regions may have been caused by contact between individuals from different areas and more extensive migration than has been previously suggested.

In the present study I used aerial surveys to estimate the abundance and examine the distribution of *T. truncatus* in Virginia coastal waters, including the Chesapeake Bay mouth. I also investigated natality periods by monthly comparison of the average percentage of calves present and residency patterns using photographic records of identifiable individuals.

METHODS

Aerial surveys were conducted during July–October 1980, and May–June 1981, from a high-winged, single-engine aircraft (U6A DeHavilland Beaver[5]) at an altitude of 152 m and at an airspeed of 147 km/h. Observers sitting in the two passenger seats searched each side of the transect for bottlenose dolphins. A recorder/navigator sitting forward of the observers and next to the pilot helped to maintain predetermined transect lines and recorded sightings which were communicated via intercom.

Upon sighting a bottlenose dolphin herd, the perpendicular distance from the flight path to the herd center was determined from calibrated, taped markings on the wing struts with the aircraft in level flight or a hand-held inclinometer. The transect was then temporarily halted and the herd circled at a lower altitude to count individuals. The herd location, direction of travel, behavior, and the number of calves were also noted. Transect lengths and the survey area were measured with a digital planimeter from NOS/NOAA navigation charts.

Depending upon the area surveyed (Fig. 1), two types of survey schemes were used. Systematic, latitudinally oriented transects were used in the Chesapeake Bay mouth (CBM) during 1980. The northern starting point for each survey was randomized, and each transect was located 7.4 km south of the previous transect. Two exceptions to this regime occurred, but in neither case was the distance between transects less than 3.7 km. Three or four transects were flown during each CBM survey and each survey covered approximately 30% of the total survey area. CBM surveys were not conducted in 1981.

Longshore surveys were flown from north to south in 1980 and 1981, parallel to the coast and 1 km offshore from Cape Charles to False Cape (32.3 km). Those conducted in 1980 were flown immediately upon completing the CBM surveys so that there was no possibility of counting herds in the longshore area that were counted during CBM surveys, except perhaps during transit between Cape Charles and Cape Henry, which was flown over open water on the shortest line between the two points. One additional survey was flown along the northern Virginia coast.

After subtracting the minimum distance from the transect that could be observed because of limited visibility directly beneath the aircraft, the perpendicular sighting distance data were truncated at 1 km. Data from all three study sites were then pooled for the calculation of $g(x)$, the detection function for line transect, and $[\hat{f}(0)]$, the probability density function of perpendicular sighting distances evaluated at the transect. In line transect the detection function $g(x)$ is the conditional probability of observing an object at perpendicular distance x from the transect line and $f(x)$ is $g(x)$ scaled to integrate to one (Burnham et al. 1980). Each survey was treated as a replicate to determine the analytical variance of $\hat{f}(0)$. Herd density was then calculated separately for each of the survey areas using $\hat{f}(0)$ estimated from the pooled sightings.

Several estimates of $\hat{f}(0)$ and its analytical variance were calculated by fitting parametric and nonparametric models to the distribution of perpendicular sighting distances using the Fortran programs TRANSECT (Laake et al. 1979) and HAZARD and HERMITE (Buckland 1985). Maximum likelihood estimates and large-sample variances were found using the procedure of Burnham et al. (1980: 135–136). The Fortran program SIZETRAN (Drummer and McDonald 1987) was used to test the hypothesis of independence between herd size and perpendicular sighting distance using a likelihood ratio test and thus determine if the detection function was biased by herd size.

Herd density was estimated as (Burnham et al. 1980, p. 18, eq. 1.3):

$$\hat{D} = n\hat{f}(0)/2L$$

[4]D. M. Burn, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, pers. commun. June 1988.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

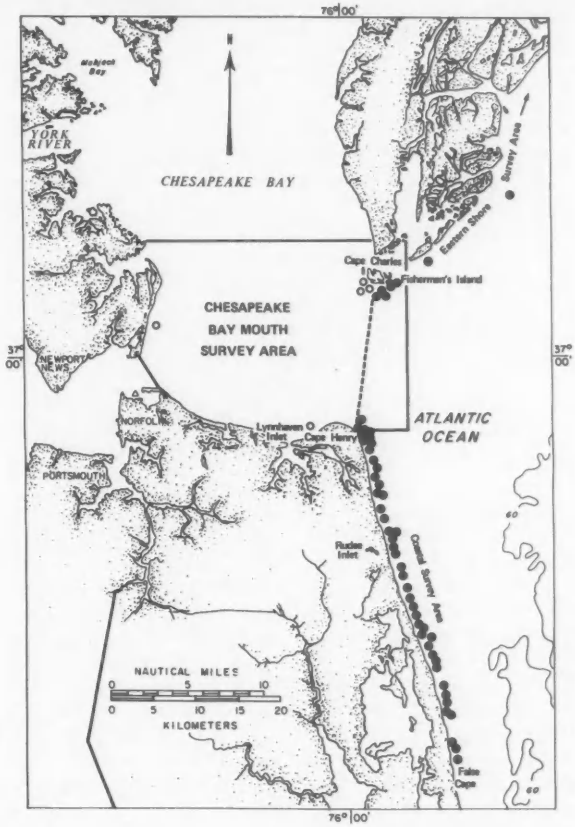

FIGURE 1.—Coastal survey areas and bottlenose dolphin sightings (closed circles) and Chesapeake Bay mouth survey area (enclosed by dark lines) with dolphin sightings (open circles). Dashed line represents transit during coastal surveys. Sightings near Fishermen's Island and Cape Henry which occurred during coastal surveys were included only in the coastal survey analyses.

where n is the number of herds detected and L is the transect length in kilometers. The variance of $\hat{D}$ was estimated as (Burnham et al. 1980, p. 51, eq. 1.17):

$$S^2(\hat{D}) = \hat{D}^2[(\hat{c}v(n))^2 + (\hat{c}v(\hat{f}(0))^2].$$

Herd size was not significantly different between study areas (Kruskal-Wallis test (K-W test), $\chi^2 = 0.9953$, df = 2, $P = 0.61$, Sokal and Rohlf 1981) and sightings were pooled to determine the overall mean herd size. Herd sizes were not normally distributed (Fig. 2) and therefore were normalized by log transformation to calculate the geometric mean (Sokal and Rohlf 1981) and its variance. Bottlenose dolphin density ($\hat{P}$) is the product of herd density ($\hat{D}$) and mean herd size ($\bar{H}$). The variance of $\hat{P}$, following Goodman (1960, p. 710, eq. 7) is

$$\hat{s}^2(\hat{P}) = \frac{\bar{H}^2 s^2(\hat{D})}{n(\hat{D})} + \frac{\hat{D}^2 s^2(\bar{H})}{n(\bar{H})} - \frac{s^2(\hat{D}) s^2(\bar{H})}{n(\hat{D}) n(\bar{H})}$$

with $n(\hat{D})$ equal to the number of herd sightings in the survey area and $n(\bar{H})$ equal to the number of herds used in the estimation of $\bar{H}$. This assumes

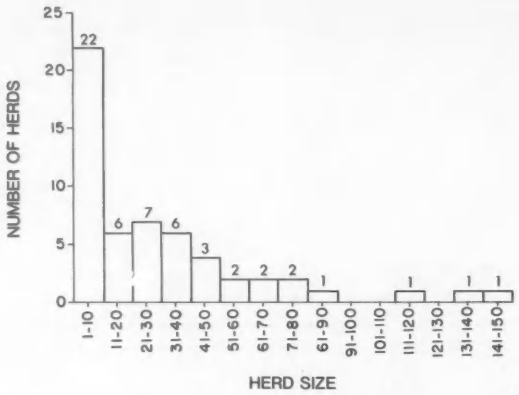

FIGURE 2.—Distribution of bottlenose dolphin herd sizes. Numbers above bars denote the number of herds in that size class.

independence between herd size and perpendicular sighting distance.

Bottlenose dolphin abundance is the product of $\hat{P}$ and the area surveyed. In the CBM area this may be extrapolated to the total area if the transects are distributed randomly with respect to dolphin sightings.

The recorder did not distinguish between observer's sightings when recording them, thus observer bias was not investigated. The effects of sea state and sun glare on detectability were not investigated. Surveys were not conducted when sea states were above two on the Beaufort scale, and it is unlikely that sea state influenced the results. However, the effect of glare reduced the observers' field of view, which decreased the number of animals detected and resulted in an underestimation of $\hat{P}$.

I conducted photographic surveys from a 7 m boat on five occasions in 1980 and six in 1981 for the purpose of identifying individual bottlenose dolphins by the shape of, or markings on, their dorsal fins. Contact prints of the 35 mm photographs were examined under a dissecting microscope at 40× magnification.

RESULTS

Six aerial surveys in the CBM averaged 119.4 km per survey, covered an area of 762 km^2, and resulted in five herd sightings of bottlenose dolphins. Ten surveys along the southern Virginia coast resulted in 49 herd sightings. Each coastal survey was 32.3 km in length and covered an area of 65 km^2. An additional survey along the northern Virginia coast was 108 km in length, covering an area of 216 km^2, and resulted in two herd sightings.

In line transect the distance at which a bottlenose dolphin herd is sighted is assumed to be independent of its size (Burnham et al. 1980; Seber 1986). Although it seems reasonable that larger herds would be detected at greater distances, analysis of herd size and sighting distance using the method of Drummer and McDonald (1987) showed no significant size-bias ($P \geq 0.05$). As a check, I also regressed herd size against perpendicular sighting distance. There was no apparent association between herd size and distance from the transect ($r^2 = 0.001$) (Fig. 3). The geometric mean herd size was 14.4 bottlenose dolphins/herd (SE = 4.0, $n = 56$).

Truncation of bottlenose dolphin sightings at 1 km resulted in the discarding of one herd sighting in the southern coastal area, none in the CBM, and one in the northern coastal area. The truncated sighting in the northern coastal area was at approximately 1,200 m from the transect and the herd was apparently feeding in the wake of a trawler, thus the sighting was atypical of other sightings during this study and probably influenced by the presence of the trawler (see Leatherwood 1975). Both sightings in this area occurred farther offshore than sightings in the other study areas.

Several parametric and nonparametric models were investigated for fit to the pooled perpendicular sighting distances (Table 1). None of the models differed significantly from the observed distance distributions (chi-square test, $P > 0.05$). The coefficient

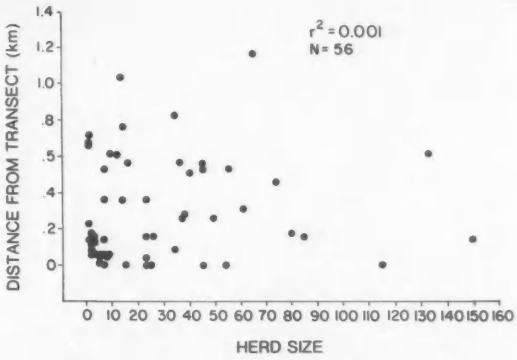

FIGURE 3.—Scatterplot of sighting distance (in kilometers) versus herd size of bottlenose dolphins. (Note that some of the points in the 1–10 size class and the interval 0–0.2 km represent more than one herd.)

TABLE 1.—Models used in calculation of the detection function $g(x)$ for bottlenose dolphin. N is the number of terms used in the model and $\hat{f}(0)$ is $f(x)$ evaluated at the transect. SE[$\hat{f}(0)$] was calculated assuming asymptotic normality with Z = 1.96.

Model	N	$\hat{f}(0)$	SE[$\hat{f}(0)$]	Reference
Hermite polynomial	3	2.849	0.441	Buckland 1985
Hermite polynomial	4	3.104	0.522	Buckland 1985
Hazard rate	na	3.004	1.345	Buckland 1985
Fourier series	4	3.323	0.551	Burnham et al. 1980
Negative exponential	na	3.216	0.936	Burnham et al. 1980
Exp. power series	2	3.649	2.198	Burnham et al. 1980
Exp. polynomial	2	3.001	0.866	Burnham et al. 1980
Half normal	na	1.950	0.398	Burnham et al. 1980

of variation of the 3-term Hermite polynomial was slightly less than that of the 4-term (0.154 vs. 0.168), but the 4-term Hermite polynomial model provided a better fit to the observed perpendicular sighting distance distribution than either the 3-term Hermite polynomial or the 4-term Fourier series models (Table 2).

The appropriate model for the observed perpendicular sighting distances should fit the data most closely near the centerline of the transect (Schweder 1977). The 4-term Hermite polynomial model closely approximates the observed sighting distances in the interval 0–200 m and also in the subsequent intervals (Fig. 4).

The nonparametric 4-term Hermite polynomial model yielded an estimate of $\hat{f}(0)$ = 3.104 (SE = 0.522). Dolphin density in the southern Virginia coastal area (3.446 dolphins/km^2) was much greater than that in the CBM area (0.159 bottlenose dolphins/km^2); however, the abundance estimates are of similar magnitude (219 vs. 121 bottlenose dolphins, respectively) due to the greater area sampled

TABLE 2.—Observed and expected distribution of bottlenose dolphin herd sightings by distance intervals perpendicular to the transect (PSD in meters) with chi-square values. Figures in parentheses are degrees of freedom. Expected values are rounded to one decimal place for clarity of presentation.

PSD (m)	Observed	4-term Hermite		3-term Hermite		4-term Fourier series	
		Expected	χ^2	Expected	χ^2	Expected	χ^2
0–200	27	27.2	0.120E-2	26.1	0.320E-1	27.4	0.698E-2
200–400	10	9.8	0.441E-2	11.1	0.117	7.4	0.913
400–600	9	9.4	0.205E-1	8.2	0.803E-1	11.6	0.593
600–700	5	4.4	0.819E-1	4.5	0.423E-1	4.9	0.273E-2
700–800	2	2.3	0.338E-1	3.3	0.819	1.9	0.197E-2
800–1,000	1	1.0	0.400E-3	0.9	0.169E-1	0.7	0.114E-2
Cumulative χ^2			0.137 (1)		1.108 (2)		1.519 (1)

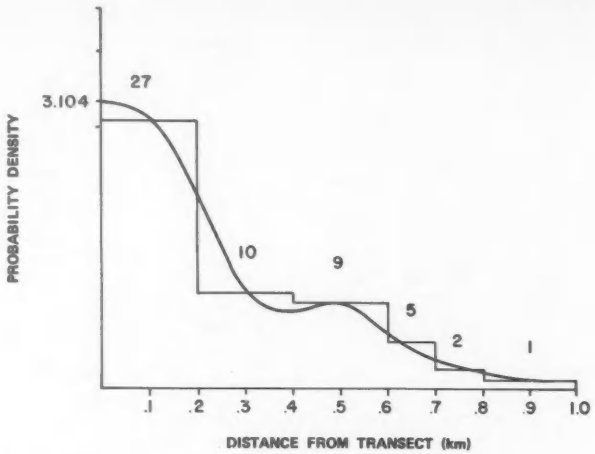

FIGURE 4.—Four-term Hermite probability density function fit to histogram of bottlenose dolphin sighting frequency and perpendicular distance (rescaled to account for the "blind spot" beneath the aircraft). Numbers above bars denote number of sightings in interval.

in the CBM (Table 3). CBM and coastal surveys were flown sequentially with no delay between them and the relatively high speed of the aircraft prevented counting of the same herd twice. Therefore, the abundance estimates in the CBM and the southern coastal survey areas may be considered additive and totaled 340 bottlenose dolphins (±104, 95% C.I.).

The survey altitude limited observations of herd composition to the percentage of calves in each herd. Bottlenose dolphins much smaller than the others and accompanied by a larger bottlenose dolphin were considered to be calves. The mean percentage of calves in all herds from all study areas peaked in June at 9.5% (SE = 0.8, n = 3) and declined thereafter until September (Fig. 5); however, there were no significant differences between months (K-W test, χ^2 = 9.1930, df = 5, $P > 0.10$). Considering the total study period, the mean percentage of calves in herds in the CBM area was 7.5% (SE = 3.2%, n = 5); in the southern coastal area, 4.3% (SE = 1.0%, n = 49); and in the northern coastal area, 9.0% (SE = 1.8%, n = 2). The mean percentage of calves in herds did not differ significantly among areas (K-W test, χ^2 = 2.8196, df = 2, P = 0.24).

TABLE 3.—Summary of aerial survey results of bottlenose dolphins. N is the number of surveys; L is the total length of transects at each location in km; and n is the number of herd sightings within one km of the transect. $\hat{D}$ is estimated herd density (herds/km^2); $\hat{P}$ is estimated dolphin density; and $\hat{A}$ is estimated dolphin abundance (standard errors in parentheses).

Survey location	N	L	n	$\hat{D}$	$\hat{P}$	$\hat{A}$	±95% C.I.
Chesapeake Bay mouth	6	717	5	0.011 (0.003)	0.159 (0.017)	121 (13)	33
Southern Virginia coast	10	323	48	0.239 (0.063)	3.446 (0.193)	219 (54)	122
Eastern Shore	1	108	1	0.014 (0.004)	0.208 (0.058)	45 (13)	—

Bottlenose dolphins were never sighted more than 1.6 km from shore during CBM surveys nor during subsequent surveys up to 8 km offshore of the coastal study area. Also, bottlenose dolphins were not found in depths greater than 10 m except in the Eastern Shore area. Plotting of bottlenose dolphin sightings (Fig. 1) shows a uniform distribution along the southern coastal area with some clusters of sightings at Cape Henry and at Cape Charles.

During 1980, seven bottlenose dolphins which were recognizable by the shape of the trailing edge of their dorsal fins were identified and photographed. In 1981, 17 individuals identified from dorsal fin photographs included 5 which had been photographed in 1980. Thus, of the 19 recognizable

individuals present during either of those two years, at least 26% were present at some time during both summers.

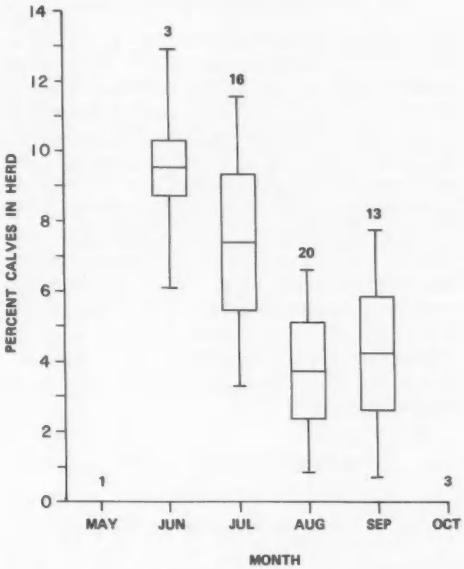

FIGURE 5.—Percentage of bottlenose dolphin calves in herds by month. Bars represent the standard error of the mean (horizontal line within bars) and vertical lines, 95% confidence intervals. Numbers above bars denote the number of herds sighted per month.

DISCUSSION

The choice of a model for $g(x)$, the probability of detecting an object at a distance x from the transect, is the primary analytical consideration in a line transect estimate of density (Burnham et al. 1980; Seber 1982, 1986). Burnham et al. (1980) thoroughly review the subject of density estimation from line transect surveys and recommended the Fourier series as a general model for $g(x)$. However, additional models which meet their criteria have since been proposed (Buckland 1985; Seber 1986). Buckland (1985) suggested the use of a model where the cosine terms in the Fourier series equation are replaced by Hermite polynomials.

Buckland (1985) warned that if the model requires four or more terms to fit the distributional data, one or more of the assumptions of line transect theory may be violated. I suggest that, in aerial surveys of cetaceans, the primary assumption that all objects on the transect are observed with a probability of one [$g(0) = 1$] is routinely violated. The diving behavior of cetaceans during different activities may vary widely, thus the probability of the animals being at the surface when the observers pass may also vary. Also, active dolphins may be more readily detected than resting dolphins. In spite of this, this assumption is somewhat less restrictive than the primary assumption of strip census which assumes that all objects within the strip are detected. If the other assumptions are met, the major consequence of failure to meet the assumption of $g(0) = 1$ is that density will be underestimated.

A further assumption is that perpendicular distances are measured without error. Even using an inclinometer, vertical motion of the aircraft and inaccuracy of the altimeter introduce error into distance measurements. Grouping distance measurements into discrete intervals is a logical way in which to compensate if the model used is robust to grouping.

The assumption of random location of transects with respect to bottlenose dolphin distribution was met by randomization of the starting point of each survey in the CBM. It is obvious from the cluster of sightings at Cape Henry and Fisherman Island that bottlenose dolphins were not distributed randomly in the coastal study area (Fig. 1). This could occur if bottlenose dolphins were counted more than once; however, their movement was slow compared with that of the observers and, because longshore surveys were flown immediately upon completion of CBM surveys, it is unlikely that dolphins were counted more than once. It is more likely that the cluster of sightings was because of an environmental factor, such as the attraction of dolphins to concentrations of prey in fronts between estuary and ocean waters.

According to Essapian (1963), mating by the bottlenose dolphin occurs in the spring and birth occurs about one year later (McBride and Kritzler 1951; Tavolga and Essapian 1957). Mead (1975), citing True (1891), stated that "Information received from the fishermen at the Hatteras fishery indicated that fetuses were generally small in September, increasing in size as the season progressed." This implies that natality occurs primarily in the spring. Townsend's (1914) data (also cited in Mead 1975) suggest an additional autumn peak in natality. The June peak in the percentage of calves agrees with those observations suggesting a spring natality peak; however, because of the slight increase in the

percentage of calves in September, a second autumn peak cannot be ruled out.

Resighting of 26% of the identifiable bottlenose dolphins in 2 successive years is evidence that some of these return to the same area. Although the probability of resighting individuals twice in 2 successive years is low if the individuals are transient, knowledge of the length of stay is required to infer seasonal residency. A study similar to that conducted on bottlenose dolphins in Argentina (Würsig and Würsig 1978) could provide information on the length of individual residency and should be considered. This would facilitate interpretation of the data presented here, as well as that gathered from currently ongoing surveys.

Because of the violation of several important assumptions, the accuracy of the density and abundance estimates reported here is difficult to assess. The CETAP (1982) summer average density estimate of nearshore *Tursiops* in the mid-Atlantic region was 0.0093 dolphins/km^2. This is much lower than my estimate of 0.159 dolphins/km^2 in the Chesapeake Bay mouth and 3.446 dolphins/km^2 in the southern coastal region. Besides differences in survey altitude and airspeed, one possible reason for this discrepancy is the larger area surveyed during the CETAP program. If the coastal *Tursiops* are generally found close to shore (within 2 km) and the area surveyed extends far beyond this distance, then the density of coastal *Tursiops* in its typical habitat will be underestimated. Alternatively, a heterogeneous coastal distribution could account for this discrepancy.

The importance of an average bottlenose dolphin density estimate which may be used as an index of abundance has recently been emphasized by an incidence of disease which resulted in the deaths of over 200 *Tursiops* along the Virginia coast and over 400 along the Mid-Atlantic Bight during the summer of 1987.[6] The rather large gap in the coastal *Tursiops* abundance data base renders assessment of the impact of the 1987 mortalities on local *Tursiops* stocks problematic. Future monitoring of the coastal *Tursiops* may provide answers as to the rate of recovery and allow assessment of the impact of future catastrophic events. A coordinated, long-term program to monitor coastal *Tursiops* abundance would permit temporal comparisons of abundance indices and provide a greater understanding of natural population fluctuations. Because the coastal *Tursiops* inhabit an area where human activity is rapidly increasing, such a monitoring program should receive high priority.

[6]J. G. Mead, Division of Mammals, Smithsonian Institution, Washington, DC, pers. commun. June 1988.

ACKNOWLEDGMENTS

I greatly appreciate the participation of R. Bowman, S. White, and especially R. A. Byles in the aerial surveys. J. G. Mead provided welcome advice and imparted to me much of his personal knowledge of the bottlenose dolphin, for which I am grateful. S. T. Buckland and T. D. Drummer graciously provided me with Fortran programs for line transect analysis. My thanks to J. A. Musick, R. A. Byles, G. P. Scott, and anonymous Fishery Bulletin reviewers who made especially helpful comments and suggestions on earlier drafts of the manuscript. This study was conducted under contract No. NA-80-FA-D-0008 to H. M. Austin from the National Marine Fisheries Service, NOAA, and an assistantship to the author from the Virginia Institute of Marine Science.

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NOTES

THE FEEDING HABITS OF TWO DEEP SLOPE SNAPPERS, *PRISTIPOMOIDES ZONATUS* AND *P. AURICILLA*, AT PATHFINDER REEF, MARIANA ARCHIPELAGO

The lutjanid snappers belonging to the genus *Pristipomoides* are among the most prized and valuable commercial fish resources in tropical and subtropical regions of the Pacific Ocean (Polovina and Ralston 1987). These fishes normally inhabit escarpments with high vertical relief. During an intensive bottom fish survey conducted at Pathfinder Reef in the Mariana Archipelago, two species of snappers, *P. zonatus* and *P. auricilla*, comprised more than 68% of the total catch (Polovina 1985). Depth of capture data on these two species demonstrated overlap in their bathymetric distribution (Polovina et al. 1985; Ralston and Williams 1988).

Numerous feeding studies have been conducted on snappers that inhabit shallow (<100 m) water; however, published information on the diets of deep slope snapper species in the tropical Pacific is nearly nonexistent (see review by Parrish 1987). Kami (1973) noted prey items for four species of *Pristipomoides* in Guam with total sample sizes ranging from one to six individuals, and Kluegel (1921) presented information on the diet of *P. filamentosus* in Hawaii based upon four fish. The present paper examines how two coexisting species, *P. zonatus* and *P. auricilla*, partition food resources. With recent efforts to expand and develop commercial fisheries for tropical snappers as well as other deep dwelling bottom fishes, there is an increasing need to recognize the resources that support these fishes. The results presented here will therefore be useful for developing fishery management strategies and will lead to a better understanding of the ecology of tropical demersal communities.

Methods

Stomach and spew samples from 106 *P. zonatus* and 72 *P. auricilla* were collected at Pathfinder Reef during an intensive fishing experiment on 10–19 April and 5–7 May 1984. Located in the Mariana Archipelago at lat. 16°30′N, long. 143°05′E, Pathfinder Reef is a circular, volcanic pinnacle rising to about 16 m beneath the surface. The fishes, ranging from 30.2 to 44.4 cm fork length ($\bar{x}$ = 38.4 cm, standard deviation = 2.81), were caught with hook and line on hydraulic-powered gurdies. The terminal rig and gurdy specifications are described in Uchida and Uchiyama (1986). While fishing, the vessel was usually allowed to drift over the banks and steep slopes, targeting species in the 150–275 m depth range. Our study species were captured mainly in depths between 180 and 220 m. Fishing was conducted around the entire perimeter of the bank during daylight hours (Polovina 1986).

Typical of feeding studies conducted on deepwater species with swimbladders, regurgitation of stomach contents posed serious problems (Bowman 1986). The rapid ascent to the surface forced most of the stomachs to evert and lose an unknown quantity of the contents. Many food items, however, were caught in the throat or gill rakers, picked out, and saved. These items, referred to as spews, and full stomachs were frozen and returned to the laboratory for analysis.

Laboratory procedures for examination of the samples were similar to those employed by Harrison et al. (1983). Briefly, food samples were sorted, counted, and identified to the lowest practical taxon. The volume of prey items was measured by water displacement. Fishes were predominantly identified by osteological and external anatomical characters and morphometrics. Invertebrates were identified by undigested hard parts and external morphological features including shells for gastropods and exoskeletons for crustaceans.

To analyze the data, we used percent frequency of occurrence to provide a qualitative picture of the food spectrum and percent volume of prey to describe relative biomass of prey items (Hyslop 1980). Because a high percentage of the diets was composed of urochordates, we did not employ any numerical analysis of the prey items. These pelagic, colonial tunicates (all *Pyrosoma* spp.) did not occur in discrete units and were thus difficult to count.

An interspecific comparison of the two snapper species requires some measure of diet overlap and niche breadth. Diet overlap (C_λ) was computed by using the formula developed by Morisita (1959) and

modified by Horn (1966). C_λ is formulated as

$$C_\lambda = \frac{2 \sum_{h=1}^{s} p_{ih} \cdot p_{jh}}{\sum_{h=1}^{s} p_{ih}^2 + \sum_{h=1}^{s} p_{jh}^2};$$

where p_{ih} and p_{jh} are the biomass proportions of a prey item h in the diets of species i and j, respectively, and s is the total number of major prey taxa in the food spectrum. C_λ varies from zero, when there is no overlap between the diets of species i and j, to one, when all prey items are in equal proportions. Niche breadth (B) for each species was computed by using the formula developed by Levins (1968):

$$B_i = \frac{1}{\sum_{h=1}^{s} p_{ih}^2};$$

where again, p_{ih} is the biomass proportion of a prey item h in the diet of species i and s is the total number of major prey taxa. The breadth values range from one, when prey items consist only of one category, to s, when all food items are in equal proportion in the same diet. These breadth values were then normalized as $B_n = B/s$, which ranges from a value of zero, representing the most uneven distribution of prey composition in the diet, to one, representing a totally even distribution. For the calculation of both breadth and overlap indexes, only prey items identified at least to the family level were used.

Results

The diets of *P. zonatus* and *P. auricilla* differed considerably from each other (Table 1). By volume, the 106 food samples from *P. zonatus* collected for this study were composed of 59.0% invertebrates and 41.0% fishes. The dominant invertebrate prey included the pelagic tunicate *Pyrosoma* spp. and galatheid crabs, nearly all *Munida japonica*. The most frequently occurring fishes in the diet were the ophichthid eel, *Shultzidia johnstonensis*, and the symphysanodontids *Symphysanodon maunaloe* and *S. typus*. In general, *P. zonatus* preyed heavily upon benthic organisms. Many of the prey items, such as echinoderms, octopods, and the various benthic crustaceans, must have been captured at the substratum. Conversely, the 72 food samples from *P. auricilla* were composed of 88.2% invertebrates and 11.8% fishes by volume; all were predominantly pelagic forms. Major invertebrate prey included the pelagic heteropod *Atlanta* spp., the pelagic tunicate *Pyrosoma* spp., and numerous species of cavolinid pteropods. Few fishes, most of them small and unidentifiable, were eaten by this snapper species.

The dietary overlap value (C_λ) was calculated to be 0.04. Based on the Langton (1982) convention of 0.00–0.29 as the low overlap, 0.30–0.60 as the medium overlap, and >0.60 as the high overlap, very little overlap occurred between the diets of the two snappers at Pathfinder Reef.

The niche breadth values (B) calculated for the two species indicated *P. zonatus* had a higher food breadth (3.82, s = 10) than *P. auricilla* (2.05, s = 6), suggesting more food specialization among the latter. Evenness in the proportion of the diet attributed to each prey type, however, was similar for the two species (B_n = 0.38 in *P. zonatus*; B_n = 0.34 in *P. auricilla*).

Discussion

As previously mentioned, a few fragmentary reports (cf. Parrish 1987) from various localities have addressed the trophic relationships of any tropical snapper inhabiting waters deeper than 100 m. He further attributes this lack of information to the normally remote fishing localities and, most of all, to the loss of stomach contents through regurgitation during capture.

The problem of regurgitation has plagued trophic studies of demersal fishes, regardless of whether fishing involved trawls (Mauchline and Gordon 1984; Clark 1985; Bowman 1986) or hook and line (Kluegel 1921; Forster et al. 1970; Seki 1984). Likewise, most food samples for our study were salvaged, regurgitated spewings retained in the mouth, throat, or gill rakers of the fishes. It is possible that the material occurring as spews may consist predominantly of certain prey items more likely retained because of size or some morphological structure, thereby resulting in a biased interpretation of the diet. We nevertheless employ the assumption that what is recovered is representative of the diets at the time of capture.

Based upon depth of capture information, *P. zonatus* and *P. auricilla* occupy nearly the same habitat, and considerable spatial overlap occurs in their foraging zones (Polovina 1986; Ralston and

Williams 1988). During submersible dives at Johnston Atoll, Ralston et al. (1986) verified this cohabitation with visual observations of the two species. *Pristipomoides zonatus* were observed between 215 and 250 m (median, 230 m) and *P. auricilla* between 205 and 295 m (median, 240 m). Our dietary analysis suggests that these two demersal species partition food resources by selecting prey from different microhabitats. *Pristipomoides zonatus* is best described as a demersal carnivore, with its diet containing benthic and demersal invertebrates together with tunicates and small fishes. In contrast, *P. auricilla* feeds primarily on large pelagic plankton, as evidenced by the abundance of heteropods, pteropods, and tunicates among the prey items. Kami (1973) also found tunicates (*Pyrosoma* spp.) in four of the five *P. auricilla* food samples in Guam. The differences in diet composition are consistent with the suggestion, based upon catch rates and the taking of a baited hook, that *P. zonatus* is the more aggressive predator of the two species (Polovina 1986).

Although our study revealed little overlap between the diets of *P. zonatus* and *P. auricilla*, the common occurrence of *Pyrosoma* spp. in the diets of both species seems significant. Similarly, these tunicates were also found among the stomach contents of three other congeneric species (Kami 1973; Parrish 1987). Kashkina (1987) reported intensive predation on pyrosomes, as well as salps, among

TABLE 1.—Diet composition of *Pristipomoides zonatus* and *P. auricilla* at Pathfinder Reef, Mariana Archipelago.

	Pristipomoides zonatus (*N* = 106)		*Pristipomoides auricilla* (*N* = 72)	
Species	% volume	% frequency	% volume	% frequency
Invertebrates				
Hydrozoa				
Siphonophora	—	—	3.2	20.8
Ctenophora	0.3	0.9	—	—
Polychaeta	0.3	0.9	5.4	15.3
Gastropoda	0.1	0.9	0.3	4.2
Atlantidae	—	—	0.9	12.5
Cavolinidae	0.2	4.7	38.1	72.2
Cephalopoda	0.3	0.9	7.4	2.8
Teuthoidea	—	—	0.2	1.4
Octopoda	0.1	0.9	—	—
Crustacea	2.6	10.4	5.5	44.4
Stomatopoda	0.3	0.9	0.3	1.4
Euphausiacea				
Euphausiidae	—	—	0.7	4.2
Decapoda				
Caridea	0.5	2.8	0.3	2.8
Pandalidae	1.2	2.8	—	—
Palinura	—	—	0.7	1.4
Anomura				
Galatheidae	19.6	28.3	—	—
Brachyura	17.1	13.2	0.2	1.4
Echinodermata				
Ophiuroidea	0.1	0.9	—	—
Tunicata				
Pyrosomatidae	16.3	34.9	25.0	37.5
Fishes				
Osteichthyes				
(Unid. fishes)	16.3	22.6	8.7	16.7
Anguilliformes	8.2	7.6	—	—
Ophichthidae	8.6	10.4	—	—
Myctophiformes	—	—	2.5	1.4
Ophidiiformes				
Ophidiidae	0.1	0.9	—	—
Perciformes				
Serranidae	4.0	1.9	—	—
Symphysanodontidae	3.1	5.7	—	—
Chaetodontidae	0.1	0.9	—	—
Gempylidae	—	—	0.6	2.8
Tetraodontiformes				
Balistidae	0.6	0.9	—	—

numerous pelagic and demersal fish species. Originally thought to be of little nutritional value, these tunicates have been found to contain filtered concentrations of phytoplankton and microzooplankton, thereby elevating the preys' food value. Regional and highly localized oceanographic processes will affect the distribution of such potential planktonic prey, and exploitation of these resources may influence the local distribution of predator species (Brock and Chamberlain 1968; Bray 1981). Deepwater snappers are most abundant on slopes of upcurrent exposure and near underwater headlands at Johnston Atoll (Ralston et al. 1986). These abundance patterns were attributed to planktonic concentrations created by mesoscale oceanographic processes as noted with other fishes on bank or slope habitats (Isaacs and Schwartzlose 1965; Pereyra et al. 1969).

Polovina (1986) suggested that fishing may selectively deplete one species, such as *P. zonatus*, preferentially over another (*P. auricilla*) and thereby alter the species composition in a given locality. With the small degree of dietary overlap between the two species in this study, such selective removal of *P. zonatus* will decrease predation pressure on the demersal prey resources of this species and, as evidenced in Larson (1980), may ultimately allow greater niche breadth for coexisting predator species.

In conclusion, this study has provided qualitative insight into dietary habits of two sympatric, deepwater species and has permitted some inferences regarding their ecology. Much more study is needed to comprehend fully the role of these predators in the ecosystem. Logistical constraints, including the problem of regurgitation, will continue to make quantitative assessments of diet a difficult task until new capture methodologies are developed. However, the rewards in improved understanding of deepwater ecology and increased ability to manage these valuable stocks suggest that the efforts will be justified.

Acknowledgments

We thank G. W. Boehlert, R. E. Bowman, C. B. Grimes, J. D. Parrish, J. J. Polovina, S. Ralston, and the two anonymous reviewers for their helpful comments on various drafts of the manuscript. This paper is a result of the Resource Assessment Investigation of the Mariana Archipelago at the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA.

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SEASONALITY AND DEPTH DISTRIBUTION OF LARVAL FISHES IN THE NORTHERN GULF OF MEXICO ABOVE LATITUDE 26°00′N

Justification and Methods

Information on early life stages of fishes is important for a better understanding of recruitment processes and for the proper management of fisheries. Knowledge of seasonal occurrence and depth distribution of larval fishes is essential for planning and scheduling ichthyoplankton cruises (Colton et al. 1979) and juvenile surveys, so that sampling for target species can be concentrated during periods and at depths where effort will be most effective (Saville 1964). In addition, knowledge of the seasonal occurrence of early life stages is an important aid in identifying larvae. Because eggs and yolk-sac larvae are planktonic for only a relatively few days after being spawned, the presence and distribution of early life stages also suggests proximity of adult spawning concentrations (Houde 1974), aiding the definition of spawning areas and seasonal spawning migrations of adults. Since some commercial and recreational fisheries (e.g., red drum, *Sciaenops ocellatus*, and black drum, *Pogonias cromis*) exploit spawning aggregations, encroachment on these aggregations could have an adverse impact on the fishery.

Colton et al. (1979) summarized larval seasonality data and spawning areas for marine continental shelf fishes between Nova Scotia and North Carolina; whereas, Herrema et al. (1985) inferred spawning seasons of coastal fishes off eastern Florida based on examination of enlarged gonads. The seasonal occurrence of larvae of many species from the northern Gulf of Mexico (GOMEX), however, is not well documented. The northern GOMEX is herein defined as waters north of lat. 26°00′N; this area approximates the U.S. Fishery Conservation (i.e., Exclusive Economic) Zone. For discussion, the study area was subdivided into three regions (Fig. 1) based on longitude as follows: eastern GOMEX (waters east of long. 86°00′W), central GOMEX (those between 86°00′W and 94°00′W), and western GOMEX (waters west of 94°00′W). Seasonality data are scattered throughout the grey literature, and many studies have focused on either select taxa or are limited in spatial or temporal coverage. The most comprehensive studies of the larval ichthyofauna community in the northern GOMEX were those of Houde et al. (1979) from continental shelf waters

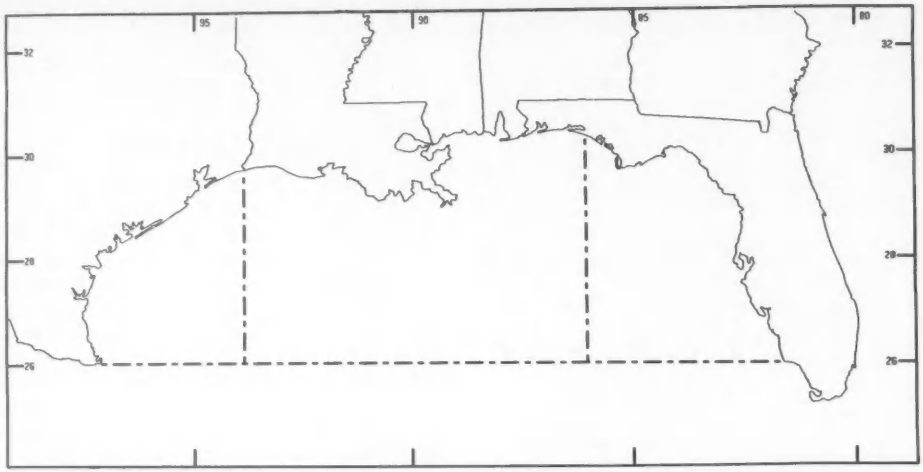

FIGURE 1.—Location of the northern Gulf of Mexico (GOMEX) and its subregions. Studies conducted in waters east of long. 86°00′W are considered northeastern GOMEX, those between 86°00′W and 94°00′W are north-central GOMEX, and west of 94°00′W are northwestern GOMEX.

off west Florida, and Finucane et al. (1977, 1979b) from the south Texas outer continental shelf. Ditty (1986) presented data on seasonality of larval fishes from neritic continental shelf waters off Louisiana that included a discussion of peak seasonal occurrence of abundant taxa; however, those data were limited in areal coverage, and there were significant gaps in the temporal occurrence of many taxa. Therefore, data on larvae of approximately 200 coastal and oceanic fishes from 61 families were compiled from unpublished plankton surveys[1], as well as other published studies from throughout the northern GOMEX, to further clarify the seasonality and peak seasonal occurrence (Table 1), and depth distribution (Table 2) of larval fishes from this area. Since the occurrence of early developmental stages of fishes suggests recent spawning (Colton et al. 1979; Ruple 1984), only studies that primarily collected larvae <10 mm SL were used. Because the taxonomy of larvae of many northern GOMEX fishes (e.g., most exocoetids, blennies, and gobies) are poorly understood, no attempt was made to compile seasonality or depth distribution data for these taxa or for anguilliform, myctophiform, or salmoniform fishes; other poorly understood taxa (e.g., engraulids and cynoglossids) were assigned only to genus.

[1]Louisiana Department of Wildlife and Fisheries, P.O. Box 98000, Baton Rouge, LA 70898-9000.

Discussion

Although not all northern GOMEX ichthyoplankton studies were readily comparable because of differences in gear and tow type, plankton net mesh size, and seasonal and areal coverage (Table 3), few major discrepancies in either seasonality or peak seasonal occurrence of larvae resulted from such differences. For example, Pearson (1929) suggested a secondary spawning from late July to November for black drum off Texas, but these dates have not been reported from elsewhere in the literature. Likewise, Finucane (1976) reported round scad, *Decapterus punctatus*, <6 mm SL in December–January, but based on sampling at the same location in subsequent years (Finucane et al. 1977, 1979b) and the seasonal occurrence of this species as suggested by others (Table 1), these may have been larvae of the rough scad, *Trachurus lathami*, rather than those of round scad. Houde et al. (1979) collected larvae of Spanish sardine, *Sardinella aurita*, during all months of their Florida continental shelf survey; however, their winter occurrences of Spanish sardine were only from the southern part of the survey area (i.e., <26°00′N). This may account for the dis-

TABLE 1.—Seasonality (X) and peak seasonal occurrence (*) of larval fishes (<10 mm SL) in the northern Gulf of Mexico (GOMEX) above lat. 26°00′N. Sources 1–31 and 75 are studies conducted in the northeastern GOMEX (waters east of long. 86°00′W); 33–59 and 74, north-central GOMEX (those between 86°00′W and 94°00′W); 61–73, northwestern GOMEX (waters west of 94°00′W); and 23, 25, 32, 48, 60, and 76–80 are Gulf-wide studies. Assignment of taxa to Families follows Robins et al. (1980) except *Epigonus* sp. and *Symphysanodon typus* which follows Johnson (1984). Numbers in Source, see end of table.

Family	Taxa	J	F	M	A	M	J	J	A	S	O	N	D	Source
Elopidae	*Elops saurus*	X	X	X	X	X		X		X	X	X		1,2,41,54,61,63,66
Albulidae	*Megalops atlanticus*						X	X	X					2,6
	Albula vulpes					X	X							54,66
Clupeidae	*Brevoortia* spp.	X	X	X	X	X					X	X	X	1–3,61–63
	B. patronus	*	*	X	X					X	X	X	*	33,40–42,46,47,49,53,55, 57–59,61–63,66,69,74
	B. smithi	X	X	X									X	5,55
	Etrumeus teres	*	*	*	X	X	X					X	X	2,5,12,29,40,41,43,50–52, 59,61,63,66,68
	Harengula jaguana			X	X	*	*	*	*	X	X	X		1–3,5,30,40,46,47,50–53, 56–59,61–63,66,68,69
	Opisthonema oglinum			X	X	*	*	*	*	X	X	X		2,5,31,40,46,50–52, 56–59,61–63,68,69
	Sardinella aurita			X	X	X	X	X	X	X	X	X		2,22,50–52,56,59,61, 63,68
Engraulidae	*Anchoa* spp.	X	X	*	*	*	*	*	*	*	X	X	X	1–3,23,25,40,41,46,47, 53,56–59,61–64,66,68,69
	Anchoviella / Engraulis	X	X	X	X	X	X	X	X	X	X	X	X	40,41,46,61–63,68
Gobiesocidae	*Gobiesox strumosus*	X	X	*	*	*	X	X	X	X	X	X	X	1,3,40,41,46,47,56,58, 59,66,68
Ogcocephalidae	*Ogcocephalus* sp.					X			X	X				68
Bregmacerotidae	*Bregmaceros atlanticus*	X	X	X	X	X	X	X	X	X	X	X	X	2,4,40,59,61–64,68
	B. cantori	X	X	X	X	X	X	X	*	*	*	*	X	2,4,40,59.64
	B. houdei	X	X			X	X	X	*	*	*	*		2,4,64
	B. macclellandi	X	X			X			X	X	X	X		2,4
Gadidae	*Urophycis* spp.	X	X	X								X	X	2,40,41,57.59,61–63,68
	U. cirrata	X												64
	U. floridanus	X	X											63
Ophidiidae	*Brotula barbata*	X										X	X	40,59,64
	Lepophidium spp.	X	X	X	X	X	X	X	X	X	X	X	X	18,40,59,63,68
	Ophidion spp.	X	X	X	X	X				X	X	X	X	40,59,61–63,68
	O. selenops		X	X	X	X	X	X	X	X	X	X		18,40
	Ophidion Type 1		X	X	X	X	X	X	X	X	X	X		18
	Ophidion Type 2		X	X	X	X	X	X	X	X	X	X		18
	Otophidium omostigmum		X	X	X	X	X	X	X	X	X	X		18,68
Carapidae	*Carapus bermudensis*	X	X			X	X	X	X	X	X	X		2,63
	Echiodon sp.	X	X		X	X	X	X	X	X	X	X		2,64
Exocoetidae	*Hemiramphus balao*		X						X			X		2
	H. brasiliensis					X	X	X						2
	Hyporhamphus unifasciatus	X	X			X	X	X	X	X		X		2,40,69
Belonidae	*Ablennes hians*							X			X			62
Atherinidae	*Membras martinica*				X	X	X	X						2,40,41,46,47,58,69
Holocentridae	*Adioryx vexillarius*											X		2
	Holocentrus sp.					X								40
Caproidae	*Antigonia* spp.		X			X			X			X		2
	A. capros								X					2
Trachipteridae	*Trachipterus* sp.		X											59
Fistulariidae	*Fistularia* sp.					X								2
Centriscidae	*Macrorhamphosus scolopax*	X	X											2,40,41,59,63,64
Serranidae	*Anthias* spp.	X	X	X	X	X	X	X	X	X	X	X	X	2,41,61,63,64
	Centropristis spp.	X	X	X	X	X		X		X	X	X	X	41,53,59,61–64,68
	C. striata	X	X	X		X				X	X	X		2,7
	Diplectrum spp.	X	X	X	X	*	*	*	*	X	X	X	X	53,59,61–64,68
	D. formosum	X	X	X	*	*	X	X	*	*	X	X		2,7
	Epinephelus spp.	X	X			X	X	X	X	X	X	X		2,64,68
	Gonioplectrus hispanus									X				64
	Hemanthias aureorubens	X	X			X	X	X	X			X		2
	H. leptus		X											2,40
	H. vivanus	X	X	X	X	X	X	X	X	X	X	X	X	2,61,63,64
	Holanthias martinicensis										X	X		64
	Liopropoma spp.	X			X	X	X	X	X	X	X	X		2,61,63,64
	Myctoperca spp.				X									64
	Plectranthias garrupellus											X		2
	Serraniculus pumilio					X	*	*	*	*	X	X		2,7,40,61–63
	Serranus spp.	X	X		X	X	X	X	X	X	X	X	X	2,63,64,68

TABLE 1.—*Continued.*

Family	Taxa	J	F	M	A	M	J	J	A	S	O	N	D	Source
Grammistidae	*Pseudogramma gregoryi*					X	X	X						2
	Rypticus spp.		X			X	X	X	*	*	X	X		2,7,40,53,61–63,68
	R. saponaceus					X	X	X	X	X				61–63,68
Priacanthidae	*Priacanthus* spp.	X	X	X	X	X	X	X	X			X		2,32,64
	P. arenatus					X								64
	P. cruentatus					X				X				64
	Pristigenys alta						X	X	X	X				2,32
Apogonidae	*Apogon* sp.							X						41
Epigonidae	*Epigonus* sp.											X		64
Malacanthidae	*Caulolatilus* spp.	X	X	X	X	X	X	X	X	X	X	X	X	2,61,63,64
	C. cyanops	X								X				2
Pomatomidae	*Pomatomus saltatrix*				X						X	X	X	40,59,61,63,64,67
Rachycentridae	*Rachycentron canadum*				X	X	X	X	X	X				2,37,62,63
Carangidae	*Alectis crinitus*							X	X	X	X			48,62
	Caranx sp.	X	X	X	X	X	X	X	X	X	X	X	X	2,8,61,63,68,69
	C. crysos			X	X	X	*	*	*	X	X	X		2,8,24,41,50–52,61
	C. hippos/latus				X	X	X	X	X					32,48,60,69
	Chloroscombrus chrysurus				X	X	*	*	*	*	X			1–3,8,40,41,46,47,50–53, 56–59
	Decapterus punctatus			X	*	*	*	*	*	*	X	X		2,8,10,24,40,50–53,59, 61–63,68
	Elagatis bipinnulata					X	X	X	X	X	X			2,56,59
	Hemicaranx amblyrhynchus					X	X	X	X	X	X			48,66
	Oligoplites saurus				X	X	*	*	*	X	X	X		1–3,8,10,32,40,41,46,48, 53,56,59–61,68,69
	Selar crumenopthalmus				X	X	X	X	X	X	X			32,40,48,53,59,60
	Selene spp.					X	X	*	*	*	X	X		2,8,10,32,40,41,48,53, 59–61,63,68
	Seriola spp.	X	X	X	X	X	X	X	X	X	X	X	X	2,8,32,40,48,56,59,60, 63,68
	Trachinotus spp.				X	X	X	X	X	X				2,8,32,47,48,61,63
	T. carolinus					X	X	X	X					32,41,48,60,66
	T. falcatus/goodei				X	X			X					48,60
	Trachurus lathami	*	*	X	X	X						X	X	2,8,23,40,41,50–52,59, 61–63,68
Coryphaenidae	*Coryphaena* spp.					X	X	X	X	X	X	X		2,41,61,64
	C. equisetis				X	X	X	X	X	X	X			2,17,23,25,40
	C. hippurus		X	X	X	X	X	X	X	X	X	X		2,17,23,25
Lutjanidae	*Etelis oculatus*							X	X	X	X	X		62,63
	Lutjanus spp.				X	X	*	*	*	X	X	X		2,40,53,59,61,63,64
	L. campechanus					X	X	X	X	X	X	X		62,64,73
	Pristipomoides aquilonaris		X			X	X	X	X	X	X	X		2,64
	Rhomboplites aurorubens	X				X	X	X	X	X	X	X		2,64
Acropomatidae	*Symphysanodon typus*		X			X						X		2
Gerreidae	*Eucinostomus* spp.				X	X	X	X	X	X	X	X		40,47,53,59,61–63,66
Haemulidae	*Haemulon* spp.					X	X	X	X					61,63
	Orthopristis chrysoptera	X	X	*	X	X								2,40,46,47,59,66,69
Sparidae	*Archosargus probatocephalus*	X	*	*	*	X								1,2,40,47,48,53,59,60, 69,70
	Diplodus holbrooki	X	X	X	X	X								2,68
	Lagodon rhomboides	*	*	X	X						X	X	*	1–3,11,40,41,46–48,53, 56,57,59,60,62,63,66,68, 69
	Pagrus pagrus	X	X			X								2,68
	Stenotomus caprinus	X											X	48,61
Sciaenidae	*Bairdiella chrysoura*			X	*	*	*	*	*	X	X			1–3,32,39–41,46,47,53, 57–59,62,63,66,69,71
	Cynoscion arenarius		X	*	*	X	X	*	*	X	X			1–3,32,34,35,39,40,46, 53,56–59,61,63,68,69,71
	C. nebulosus		X	X	*	*	*	*	*	X	X			1–3,32,35,39–41,46,47, 53,56–59,68–72
	C. nothus					X	X	X	X	*	*	X		2,32,39–41,46,53,56,59, 61–63,68
	Larimus fasciatus				X	X	X	X	X	*	X	X		34,39–41,46,53,56,58,59, 61–63,69
	Leiostomus xanthurus	*	X	X	X						X	X	*	1–3,34,39–41,44,46,47, 53,56–59,61–63,66, 68–71,74

TABLE 1.—*Continued.*

Family	Taxa	J	F	M	A	M	J	J	A	S	O	N	D	Source
	Menticirrhus spp.		X	X	X	X	X	X	X	X	X	X	X	1–3,32,34,39–41,46,47, 53,56–59,61–63,66,68,69
	Micropogonias undulatus	*	X	X	X					X	*	*	*	1–3,34,39–41,44,46,47, 53,56–59,61–63,66, 68–71,74
	Pogonias cromis	X	*	*	*	X							X	1–3,34,39,40,46,47,56, 58,59,61,63,66,68–70,72
	Sciaenops ocellatus								X	*	*	X		1,28,39,40,46,47,53,56, 58,59,61,63,66,69,70,72
	Stellifer lanceolatus				X	X	X	X	X	X	X			32,39–41,46,53,56–59, 66,69
Mullidae	*Mullus auratus*					X								2
Kyphosidae	*Kyphosus* spp.	X	X		X	X	X	X				X		2,61,63
Ephippidae	*Chaetodipterus faber*				X	X	*	*	*	X				40,41,46,47,53,56,57,59, 61–64,66,68
Pomacentridae	*Abudefduf saxatilis*							X						63
Mugilidae	*Mugil* spp.	X	X	X	X	X	X	X	X	X	X	X	X	2,61,63,68
	M. cephalus	*	*	X	X						X	X	*	40,41,44,47,53,57,59, 61–64,69,71
	M. curema				X	*	*	*	X					40,46,47,57,59,63,64,68
Sphyraenidae	*Sphyraena* spp.				X	X	*	*	*	X	X	X		40,46,53,57,59,61–64,66, 68
	S. barracuda					X	X	X	X	X				2,64
	S. borealis		X	X	X	X								2,61,68
	S. guachancho					X	X	X	X	X				2,61,63
Polynemidae	*Polydactylus octonemus*				X									64
Opistognathidae	*Lonchopisthus macrognathus*					X								68
	Gnathagnus egregius	X	X											63
Callionymidae	*Callionymus* spp.					X				X				61,68
	C. bairdi	X												59
	C. pauciradiatus									X	X	X		40,59
Microdesmidae	*Microdesmus* spp.			X	X	X	X	X	X	X	X	X		2,40,46,57,59,61–64,68
Acanthuridae	*Acanthurus* spp.	X	X			X			X	X	X	X		2,64
Gempylidae	*Gempylus serpens*				X							X		2,61
	Nealotus tripes	X						X						2,41
	Nesiarchus nasutus	X	X									X		2,59
	Diplospinous multistriatus	X	X	X	X	X	X	X		X		X	X	2,40,41,59,61,63
Trichiuridae	*Lepidopus* sp.							X						61
	Trichiurus lepturus	X	X	X	X	X	X	X	X	X	X	X	X	40,41,56,59,61,63,68
Scombridae	*Acanthocybium solanderi*				X	X	X	X	X	X				2,25
	Auxis spp.	X	X	X	X	*	*	*	*	*	X	X		2,21,23,25,32,40,59,61, 63,64,68,79
	Euthynnus alletteratus				X	*	*	*	*	*	X	X		2,21,23,25,32,40,53,57, 59,61–64,68,79
	E. pelamis				X	X	X	X	X	X	X			2,21,23,25,32,40,61,63, 64,79
	Sarda sarda							X						53
	Scomber japonicus	X	X	X	X	X	X			X	X	X		2,32,40,61,63,68
	Scomberomorous cavalla					X	X	X	*	*	X	X		2,21,23,25,27,32,40, 50–52,59,61–65,68
	S. maculatus				X	X	X	X	*	*	X			2,23,25,27,32,40,50–53, 56,57,59,61–63,65,66,68
	T. albacares				X	*	*	*	X	X				40,63
	T. atlanticus				X	*	*	*	X	X	X	X		2,21,23,25,32,40,61,63, 64,79
	T. thynnus				X	X	X							2,21,23,25,32,40,61,64, 68,76–78,80
Xiphiidae	*Xiphias gladius*	X	X	X	*	*	*	X	X	X	X	X	X	19,23,25,64,79
Istiophoridae	*Istiophorus* sp.				X	X	X	X	X					2,16,23,25,61–64
Stromateidae	*Ariomma* spp.	X	X	X	X	X	X	X	X			X	X	2,40,41,57,59
	Cubiceps pauciradiatus	X	X	X	X	X	X	X	X	X	X	X	X	2,40,41,59,61,63,64
	Hyperoglyphe bythites					X	X	X	X					36
	Nomeus gronovii	X	X											40,41
	Peprilus paru				X	X	*	*	*	X	X	X		2,32,38,40,41,53,56,57, 59,61–63,66
	P. burti	*	*	*	X	X	X	X	X	X	X	*	*	2,32,38,40,41,53,57,59, 61–64,66,68
	Psenes spp.		X						X			X		2
	P. cyanophrys					X								2

TABLE 1.—*Continued.*

Family	Taxa	J	F	M	A	M	J	J	A	S	O	N	D	Source
	P. pellucidus	X	X							X	X	X		2
	Tetragonurus atlanticus	X												59
Scorpaenidae	*Scorpaena* spp.	X	X	X	X	X	X	X	X	X	X	X	X	2,40,41,53,56,57,61–63, 66,68
Triglidae	*Peristedion* spp.					X								2
	Prionotus spp.	X	X	X	X	X	X	X	X	X	X	X	X	1–3,40,41,46,53,56–59, 61–64,66,68,69
Dactylopteridae	*Dactylopterus volitans*					X								2,40
Bothidae	*Bothus* spp.	X			X	X	X	X	X	X	X	X	X	32,40,41,45,59,61–64,68
	B. ocellatus	X	X	•	•	•	X	X	X	X	X	X	X	61–63,68
	B. robinsi		X	X	X	•	•	•	•	•	•	•		2,9
	Citharichthys spp.	X	X	X	X	X	X	X	X	X	X	X	X	32,40,46,56–59,63,66,68, 69
	C. cornutus	X	X		X	•	•	•	•	X	X	X		2,9,32,40
	C. gymnorhinus	X	X			X	X	X	X	X	X	X	X	2,9,32,40,59
	C. macrops	X	X	X	X	•	X	X	X	X	X	X		2,9,26
	C. spilopterus	X	X	X	X	X		X	X	X	X	X	X	2,26,40,41,45,53,59
	Cyclopsetta spp.	X	X	X		X	X	•	•	•	X	X		32,40,41,45,61–63,68
	C. fimbriata	X	X			X	•	X	X	•	X	X		2,9,62,63
	Engyophrys senta					X	X	X	X	X	X			2,20,32,40,41,45,53,59
	Etropus crossotus				X	X	X	X	X	X	X	X		26,32,40,41,45,46,56,57, 59
	E. rimosus	•	•	•	•	X	X	X	X	X	X	•	•	2,9,26
	Monolene sessilicauda					X	X	X	X	X	X	X	X	2,9,13,32,40,61,62,68
	Paralichthys spp.	•	•	X	X					X	X	X	•	1,2,40,41,45–47, 53,57, 59,61–63,66,68–70
	Syacium spp.				X	X	•	•	•	X	X	X	X	32,40,41,45,53,59,61–64, 68
	S. gunteri						X	•	•	X	X	X	X	32,40,57,61–63,66
	S. papillosum					X	•	•	•	•	X	X		2,9,14,32,40
	Trichopsetta ventralis					X	X	X	X	X	X			2,9,15,32,40,45
Soleidae	*Achirus lineatus*		X	X	X	X	•	•	•	X	X	X		2,3,40,41,45–47,53,56, 57,59,75
	Gymnachirus sp.				X	•	•	X						61,63
	G. melas		X			X	X					X		2
	Trinectes maculatus				X	X	•	X	X	X				1,40,46,53,58,66
Cynoglossidae	*Symphurus* spp.	X	X	X	X	X	X	X	X	X	X	X	X	2,3,40,45–47,53,56–59, 61–64,66,68,69
Balistidae	*Balistes* sp.							X	X					61
	Monacanthus sp.					X				X	X			61,62,68
	M. hispidus					X	X	X		X		X		46,53,69
	M. setifer											X		40
Ostraciidae	*Lactophrys* sp.					X	X						X	66,68
Tetraodontidae	*Lagocephalus laevigatus*					X				X				68
	Sphoeroides spp.	X	X	X	X	X	X	X	X	X	X	X	X	1,2,40,41,46,53,56,57, 59,61–64,66,68,69
Molidae	*Ranzania laevis*										X			64

[1]Blanchet 1979.
[2]Houde et al. 1979.
[3]Phillips et al. 1977.
[4]Houde 1981.
[5]Houde and Fore 1973.
[6]Smith 1980.
[7]Houde 1982.
[8]Leak 1981.
[9]Dowd 1978.
[10]Aprieto 1974.
[11]Caldwell 1957.
[12]Houde 1973.
[13]Futch 1971.
[14]Futch and Hoff 1971.
[15]Futch 1977.
[16]Gehringer 1957.
[17]Gibbs and Collette 1959.
[18]Gordon 1982.
[19]Grall et al. 1983.
[20]Hensley 1977.
[21]Juarez 1976.
[22]Houde 1976.
[23]Kelley et al. 1986.
[24]Montolio 1976.
[25]Richards et al. 1984.
[26]Tucker 1978.
[27]Dwinell and Futch 1973.
[28]Peters and McMichael 1987.
[29]Houde 1977a.
[30]Houde 1977b.
[31]Houde 1977c.
[32]SEAMAP 1983.
[33]Christmas and Waller 1975.
[34]Cowan 1985.
[35]Daniels 1977.
[36]Dawson 1971a.
[37]Dawson 1971b.
[38]Ditty 1981.
[39]Ditty 1984.
[40]Ditty 1986.
[41]Ditty and Truesdale 1984.
[42]Fore 1970.
[43]Fore 1971.
[44]Fruge 1977.
[45]Kuhn 1979.
[46]Ruple 1984.
[47]Sabins 1973.
[48]SEAMAP 1985.
[49]Shaw et al. 1985.
[50]Shaw and Drullinger 1985.
[51]Shaw and Drullinger 1986.
[52]Shaw et al. 1987.
[53]Stuck and Perry 1982.
[54]Thompson and Deegan 1982.
[55]Turner 1969.
[56]Vecchione et al. 1982.
[57]Walker 1978.
[58]Williams 1983.
[59]LDWF 1983 unpubl. data.
[60]SEAMAP 1984.
[61]Finucane et al. 1977.
[62]Finucane et al. 1979a.
[63]Finucane et al. 1979b.
[64]McGowan 1985.
[65]McEachran et al. 1980.
[66]Hoese 1965.
[67]Barger et al. 1980.
[68]Finucane 1976.
[69]Allshouse 1983.
[70]King 1971.
[71]Guillen and Landry 1981.
[72]Pearson 1929.
[73]Collins et al. 1980.
[74]Sogard et al. 1987.
[75]Houde et al. (1970, cited in Phillips et al. 1977).
[76]Richards 1976.
[77]Richards 1977.
[78]Richards and Potthoff 1980a.
[79]Richards and Potthoff 1980b.
[80]McGowan and Richards 1986.

TABLE 2.—Primary depth distribution of larvae (<10 mm SL) of some abundant taxa of fishes from the northern Gulf of Mexico above lat. 26°00'N. Depths are those reported in the literature at which >75% of larvae were collected. Asterisk (*) indicates larvae are estuarine-dependent.

Taxa	Depth (m)					Source
	<25	<50	<100	50–200	>150	
Chloroscombrus chrysurus	X					1,2,3,4,5,6,8,10
Orthopristis chrysoptera	X					1
Cynoscion nebulosus *	X					1,9,10
C. arenarius	X					1,2,9,10,11
Pogonias cromis *	X					11
Archosargus probatocephalus *	X					1
Chaetodipterus faber	X					2
Peprilus paru	X					1,25,26
Anchoa spp.		X				1
Harengula jaguana		X				1,4,5,6,13
Opisthonema oglinum		X				1,4,5,6,10,29
Brevoortia patronus *		X				14,15,16,17,32
Sardinella aurita		X				1,4,6,18
Diplectrum formosum		X				1
Serraniculus pumilio		X				1
Centropristis striata		X				1
Lagodon rhomboides *		X				1
Leiostomus xanthurus *		X				1,11,19,32
Micropogonias undulatus *		X				1,11,19,20,32
Scomberomorus maculatus		X				1,4,21,22,23,24
Decapterus punctatus			X			1,3,4,6
Peprilus burti			X			25,26
Etrumeus teres				X		1,5,6,11,12,27,28,30
Caranx crysos				X		1,3,4,6
Trachurus lathami				X		1,2,3,5,30
Hemanthias vivanus				X		1
Auxis sp.				X		1,21,22,23
Euthynnus alletteratus				X		1,21,22,30
Scomberomorus cavalla				X		20,23,24
Lutjanus campechanus				X		31
Xiphias gladius					X	7,21,22
Istiophorus spp.					X	21,22
Euthynnus pelamis					X	1,21,22,23

[1]Houde et al. 1979.
[2]Ditty and Truesdale 1984.
[3]Leak 1981.
[4]Shaw et al. 1987.
[5]Shaw and Drullinger 1986.
[6]Shaw and Drullinger 1985.
[7]Grall et al. 1983.
[8]Montolio 1976.
[9]Daniels 1978.
[10]Walker 1978.
[11]Cowan 1985.
[12]Houde 1977b.
[13]Houde 1977c.
[14]Shaw et al. 1985.
[15]Fore 1970.
[16]Turner 1969.
[17]Christmas and Waller 1975.
[18]Houde 1976.
[19]Fruge 1977.
[20]Finucane et al. 1977.
[21]Richards et al. 1984.
[22]Kelley et al. 1986.
[23]Dwinell and Futch 1973.
[24]McEachran et al. 1980.
[25]Ditty 1981.
[26]SEAMAP 1983.
[27]Fore 1971.
[28]Houde 1973.
[29]Houde 1977a
[30]Finucane et al. 1979b.
[31]Collins et al. 1980.
[32]Sogard et al. 1987.
[33]Richards and Potthoff 1980b.

crepancy in Spanish sardine seasonal occurrence reported by Houde and Fore (1973) (September–February) and that found by Shaw and Drullinger (1985, 1986), Shaw et al. (1987), and this review (March–November). Finally, seasonality data reported in Ditty (1986) for larvae of finescale menhaden, *Brevoortia gunteri*, was based on specimens subsequently believed to be a morph of gulf menhaden (*B. patronus*).

In general, the seasonal occurrence of many taxa of larval fishes (i.e., scaled sardine, *Harengula jaguana*, and Atlantic thread herring, *Opisthonema oglinum*) began both earlier and extended later in studies conducted on the Florida continental shelf and southern parts of the study area than those in the northern-most GOMEX. Likewise, in studies involving bays (e.g., Phillips et al. 1977; Blanchet 1979; Williams 1983), tidal passes (e.g., King 1971; Sabins 1973; Allshouse 1983), and barrier islands (e.g., Guillen and Landry 1981; Ruple 1984), peak seasonal occurrence of larvae of some fishes was usually later than in studies conducted offshore, primarily because of the time delay necessary for shoreward migration of estuarine-dependent larvae such as Atlantic croaker (*Micropogonias undulatus*), striped mullet (*Mugil cephalus*), pinfish (*Lagodon*

TABLE 3.—Location and sampling characteristics for northern Gulf of Mexico (GOMEX) ichthyoplankton studies. For months sampled: Q = quarterly, M = monthly, S = synoptic, B = biweekly. Numbers in columns with asterisk (*) refer to footnotes. Numbers separated by semicolons refer to specific gear types.

Study	Gear type*	Mesh size (mm)	Station depths (m)	Months/freq. sampled*	Study type/ taxa studied	Tow type*	Study location
Phillips et al. 1977	2	0.363	<10	10, B	Survey	13	Tampa/Hillsborough Bay, FL
Blanchet 1979	2	0.505	2–6	11, M	Survey	14	Lower Apalachicola Bay, FL
Houde et al. 1979	1, 2	0.505	10–200	9, Q	Survey	13	Florida continental shelf
Turner 1969	4	0.571	<58	9, Oct.–Apr.	*Brevoortia*	15, 19	Eastern and central GOMEX
Williams 1983	5	0.505	<10	11, M	Survey	14, 17	Lower Mobile Bay, AL
Struck and Perry 1982	2	1.050	10	9, M	Survey	14, 17	Off Mississippi Sound
Ruple 1984	4; 6	0.505, 0.571	4–7; 0.5	12, M	Survey	14, 19; 21	Horn Island, MS
Juarez 1976	2	0.505	>183	Q, Apr.–Nov.	Scombrids	13	Central GOMEX
Montolio 1976	2	0.505	>183	Q, Apr.–Nov.	Carangids	13	Central and western GOMEX
Fore 1971	—	—	27–108	M, Dec.–Apr.	*Etrumeus*	—	Central GOMEX
Sabins 1973	8	0.480	<1.5	11, M	Survey	19, 21	Caminada Pass, LA
Fruge 1977	1, 2	0.505	<91	Nov.	*Micropogonias*	13	Mississippi River Delta to Atchafalaya Bay, LA
Kuhn 1979	1	0.505	10–91	Nov., Jan., July	Bothids	13	Mississippi River Delta to Atchafalaya Bay, LA
Ditty and Truesdale 1984	1	0.505	10–91	Jan., July	Survey	13	Mississippi River Delta to Atchafalaya Bay, LA
Walker 1978	2	0.505	10–45	July, Aug., Dec.	Survey	15, 19	Mississippi River Delta to Timbalier Bay, LA
Ditty 1986	1; 2	0.363	10; 30	11, M; 9, Q	Survey	14, 16, 17; 14	Off Caminada Pass, LA
Vecchione et al. 1982	1	0.333, 0.505	10	11, M	Survey	14, 16, 17	Southwest Louisiana off Calcasieu Lake
Cowan 1985	1	0.335	6–130	M, Dec.–Apr.	Sciaenids	18	Southwest Louisiana
Shaw et al. 1985	1	0.335	6–130	M, Dec.–Apr.	*Brevoortia*	18	Southwest Louisiana
Guillen and Landry 1981	8	1.000	<1.5	M, Jan.–Aug.	Survey	19, 21	Galveston Island, TX
McGowan 1985	1	0.333	Over reef	9, Q	Survey	13, 20	Flower Gardens Reef, TX
King 1971	4	1.000	<5	9, M	Survey	14, 16, 17	Cedar Bayou Pass, TX
Hoese 1965	2	0.086	6–50	9, M	Survey	14	Off Port Aransas, TX
Allshouse 1983	4	0.505	3–12	11, M	Survey	13	Aransas Pass, TX
Finucane 1976	2	0.250	18–135	Dec., Apr., Aug.	Survey	13	South Texas continental shelf
Finucane et al. 1977, 1979b	1	0.333, 0.505	18–182	9, M	Survey	13	South Texas continental shelf
Finucane et al. 1979a	1	0.333, 0.505	17	July, Oct., Feb.	Survey	13	Off Galveston, TX
Fore 1970	7	—	7–75	M, Sept.–Apr.	*Brevoortia*	18	Central and western GOMEX
Christmas and Waller 1975	2; 4	0.505; 1.000	2–110	9, Oct.–Apr.	*Brevoortia*	13; 14	Gulf-wide
Richards and Potthoff 1980a, b	1; 3	0.505; 0.946	>183	9, Apr.–May	Scombrids	13; 14	Gulf-wide
SEAMAP 1983–1985	1; 3	0.333; 0.946	>10	9, S	Survey	13; 14	Gulf-wide

[1]60 cm bongo.
[2]1 m met.
[3]1 × 2 m neuston.
[4]0.5 m net.
[5]1 × 0.5 net.
[6]2 × 0.5 m.
[7]Gulf-V sampler.
[8]Renfro beam trawl.
[9]Multiyear.
[10]15 months.
[11]12 months.
[12]14 months.
[13]Oblique.
[14]Surface.
[15]Subsurface.
[16]Middepth.
[17]Bottom.
[18]Stepwise oblique.
[19]Horizontal.
[20]Oblique at select depth intervals.
[21]Surf zone.

rhomboides), black drum, red drum, and gulf menhaden.

The seasonal occurrence of several taxa are known only from a few scattered specimens (e.g., cornetfish, *Fistularia* sp.; ribbonfish, *Trachipterus* sp.; cowfish, *Lactophrys* sp.; slender mola, *Ranzania laevis*; threadfish, *Polydactylus* sp.; and cobia, *Rachycentron canadum*) or a single monthly record (Table 1). Larvae of other taxa (e.g., searobins, *Prionotus* spp.; anchovies, *Anchoa* spp.; tonguefishes, *Symphurus* spp.; and pufferfishes, *Sphoeroides* spp.) were collected during all months (Table 1), reflecting the many species that comprise each genus. In general, larvae of most scombrids were collected beyond the 50 m depth contour, except Spanish mackerel, *Scomberomorus maculatus*, which occurred primarily within 50 m. Finucane et al. (1979b) collected 50% of their king mackerel, *S. cavalla*, larvae off Texas during September and found this species relatively more abundant and over greater water depths (35–183 m) than Spanish mackerel (<35 m). In the north-central GOMEX, larvae of

Spanish mackerel were more abundant than those of king mackerel, and spawning of this latter species probably occurs over shallower depths than in the northwestern GOMEX (Shaw et al. 1987). Only six larvae of king mackerel were collected by Houde et al. (1979), suggesting that this species does not use the northeastern GOMEX as a major spawning area. Larvae of cero, *S. regalis*, have not been reported from the study area. Larvae of sciaenids and engraulids occurred primarily within the 50 m depth contour, with several species of sciaenids primarily collected inside the 25 m contour (Table 2). Both sciaenids and engraulids are relatively more abundant in the north-central and northwestern than in the northeastern GOMEX (Finucane et al. 1977, 1979b; Houde et al. 1979; Richards et al. 1984; Kelley et al. 1986) (Table 4). Most larvae of clupeids occur in shelf waters of <50 m depth, except those of round herring, *Etrumeus teres*, which primarily occur beyond the 50 m contour (Table 2). Larvae of gulf menhaden are more abundant in the north-central than either the northeastern or northwestern GOMEX and occur primarily around the Mississippi River Delta (Fore 1970; Christmas and Waller 1975; Sogard et al. 1987; and others). Scaled sardine and Atlantic thread herring larvae are abundant in all three subregions of the northern GOMEX; Spanish sardine are rare in the north-central but relatively abundant in the northeastern and northwestern GOMEX (Shaw and Drullinger 1985, 1986; Shaw et al. 1987). Larvae of gulf butterfish, *Peprilus burti*, and harvestfish, *P. paru*, are most common in the north-central GOMEX (SEAMAP 1983), with only a few of their larvae (8 and 25, respectively) having been collected by Houde et al. (1979) in the northeastern GOMEX. Although gulf butterfish larvae have been collected during every month (Table 1), larvae are most common from November to March with very limited spawning during the summer (Ditty 1981; SEAMAP 1983). Houde et al. (1979) also collected >90% of both sparid and haemulid larvae inside the 50 m contour during their Florida continental shelf survey and found that although lutjanids occurred at all depths, they were most abundant from 30 to 100 m. Unlike larvae of other speciose families which primarily occurred either within (e.g., clupeids, engraulids, and sciaenids) or beyond (e.g., scombrids) the 50 m depth contour, those of bothids, carangids, and serranids were widely distributed and occurred at all depths. Larvae of swordfish, *Xiphias gladius*, and sailfish, *Istiophorus* sp., are oceanic and occurred primarily outside the 200 m depth contour; leptocephali of tarpon, *Megalops atlanticus*, and bonefish, *Albula vulpes*, were seldom collected in the study area. Of those taxa whose larvae were most abundant within the 25 m contour (Table 2), several were most commonly collected at considerably shallower depths (e.g., pigfish, *Orthopristis chrysoptera* <20 m; black drum <18 m; and spotted seatrout, *Cynoscion nebulosus* <15 m). Larvae of other taxa which occurred primarily within the 25 m contour includes leatherjacket, *Oligoplites saurus* (<20 m; Houde et al. 1979); kingfish, *Menticirrhus* spp. (<20 m; Walker 1978; Houde et al. 1979; Cowan 1985); and spottail pinfish, *Diplodus holbrooki* (<15 m; Houde et al. 1979). Larvae of hogchoker, *Trinectes maculatus*, and silver perch, *Bairdiella chrysoura*, were occasionally collected in neritic offshore studies, but were most abundant in pass/estuarine studies (e.g., Sabins 1973; Allshouse 1983).

TABLE 4.—Comparison of 10 most abundant families of larval fishes collected during major ichthyoplankton surveys of the Gulf of Mexico. Rank is based on number of individuals collected. Numbers are % of total collection.

Taxa	Finucane 1976	Finucane et al. 1977	Finucane et al. 1979b	Houde et al. 1979	Kelley et al. 1986
Engraulidae	17.4	13.5	6.2		14.6
Gobiidae	16.6	20.6	15.8	15.1	6.2
Bregmacerotidae	14.5	12.5	7.3	2.7	5.4
Clupeidae	8.5	5.0	8.1	20.5	9.6
Sciaenidae	5.3	2.1			3.1
Carangidae	4.8	3.1	3.7	3.9	4.1
Bothidae	4.6	8.4	6.1	6.4	4.4
Synodontidae	4.5	3.6	10.9	3.0	
Myctophidae	3.0	5.0	4.9	5.1	11.2
Serranidae	2.0		2.2	4.9	
Cynoglossidae			3.4		
Scombridae		1.9			
Ophidiidae				2.9	
Labridae				2.3	
Gonostomatidae					3.3
Mugilidae					2.5
Totals	81.2	75.7	68.6	66.8	64.4

In conclusion, these data represent the current knowledge of the seasonality, peak occurrence, and primary depth distribution of larval fishes in the northern GOMEX. This information provides a foundation upon which sound management decisions concerning both the commercial and recreational exploitation of spawning aggregations of fishes and the potentially adverse impact on these fisheries resulting from such exploitation can be based.

Acknowledgments

We would like to thank the Louisiana Department

of Wildlife and Fisheries and the Louisiana Offshore Oil Port (LOOP, Inc.) for providing unpublished seasonality data from 1983 plankton surveys; the Southeast Area Monitoring and Assessment Program (SEAMAP) for providing data on selected species of clupeids, priacanthids, carangids, scombrids, and bothids collected during 1982 surveys of northern GOMEX waters; and to William J. Richards for sharing information on *Peprilus burti* and *P. paru* collected during 1982 SEAMAP cruises. This paper is dedicated to Robert and Katherine Ditty whose love and support through the years are an inspiration. Louisiana State University Coastal Fisheries Institute Contribution No. LSU-CFI-87-25.

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UTILIZATION OF A WASHINGTON ESTUARY BY JUVENILE ENGLISH SOLE, *PAROPHRYS VETULUS*

The use of west coast estuaries and protected bays as nursery grounds by English sole, *Parophrys vetulus* Girard, a significant component of Pacific coast groundfish landings, has been well documented (Westerheim 1955; Kendall 1966; Smith and Nitsos 1969; Misitano 1970). From data collected off Oregon, Laroche and Holton (1979) showed that English sole also utilize nearshore areas along the open coast as nursery grounds. Krygier and Pearcy (1986) determined that estuarine dependence for juvenile English sole was indeed significant relative to the open coastal area off Oregon, although their survey design made it difficult to compare absolute abundance in these areas. In addition, the estuaries studied by Krygier and Pearcy were much smaller than the Washington estuaries of Grays Harbor and Willapa Bay, making it difficult to extrapolate their results.

In the present study our objectives were to 1) compare relative density and estimates of abundance of 0-age English sole between a Washington estuary, Grays Harbor, and the adjacent area along the open coast; 2) compare fish density between several subareas (strata) of each system; and 3) note timing of immigration to and emigration from the estuary. Specific gear was developed to efficiently sample small benthic organisms and was used in both the estuary and open coast survey areas, eliminating the need for gear selectivity intercalibration. In addition, the statistical design of the survey enabled population estimates with confidence intervals to be made for each area.

Methods and Materials

Survey Design

For this study, we specifically developed a plumb staff beam trawl with an effective width of 2.3 m. We designed it for a quantitative assessment of juvenile fishes and crustaceans closely associated with the bottom. Its fine mesh (4 mm) cod end liner retained newly settled flatfish (15–25 mm total length). A complete account of its construction, method of deployment, and field testing was given by Gunderson and Ellis (1986).

We selected two separate survey areas for the study, the Grays Harbor estuary and the adjacent nearshore area along the open coast. The estuarine survey was based on a stratified random statistical design and the open coast survey on a systematic trackline. Both areas were surveyed in 1983 and 1984.

The estuary was stratified into four geographic areas (Fig. 1). Each stratum was divided into 1 × 1 km grids (1 km intervals in the case of narrow channels), and several stations were then randomly selected with the constraint that no two be adjacent. Additional stations were added in both STR (stratum) 1 and 2 for the 1984 survey.

For the open coastal survey, three tracklines oriented perpendicular to the bathymetry were located off Copalis Head, Westport, and Willapa Bay (Cape Shoalwater) (Fig. 2). We established a systematic series of stations along each trackline at 9 m depth intervals from 9 to 64 m. Whenever wave conditions permitted, we sampled an additional station at 5.5 m. In 1984, the 64 m stations were dropped on each trackline because of consistent gear damage in 1983. Also in 1984, replicate tows were made at the 27 and 37 m stations.

Sampling Schedule

We sampled the estuary twice monthly from April through September 1983 and 1984, and a single trip was made in January 1984 for continuity. The two

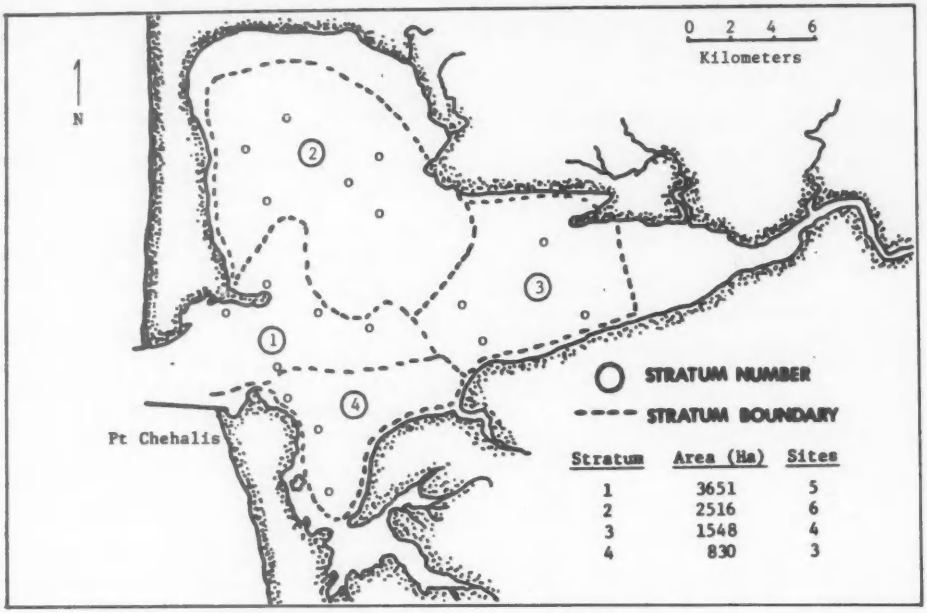

FIGURE 1.—Chart of Grays Harbor, WA, showing the four strata and random trawl sites selected from grid lines.

trips per month coincided with low tides when navigation and location of stations within the narrow channels characteristic of the North Bay and Inner Harbor would be easiest. Stations situated in the shallow, unmarked channels were sampled at low water, while stations in more navigable areas were sampled during the following periods of high water. All hauls were confined to slack tide periods so that strong tidal currents would not interfere with the operation of the beam trawl. We sampled the offshore study area once a month from April through September.

Field Techniques

Within the estuary, the plumb staff beam trawl was operated from a 6 m outboard boat, while offshore, either a 17 m or 20 m vessel was chartered. Mechanical or hydraulic winches allowed the retrieval of the beam trawl while underway, reducing escapement of captured organisms from the net.

At all stations, the beam trawl was hauled for a distance dependent on the amount of epibenthic material expected. Hauls of <10 minutes duration (200–300 m) were necessary within the estuary because the small mesh cod end liner would clog with mud and organic debris, making the net difficult to retrieve. Although the same problem existed in the open coast survey area, hydraulic lifting gear enabled hauls of up to 20–30 min duration (800–1,000 m) at most stations. We attempted to tow at 3 km/h with a scope of about 5:1; at depths <5 m, the scope was increased to 10:1.

Within the estuary, marker buoys were deployed where we estimated the trawl started and stopped fishing. The distance fished was determined by measuring between buoys with an optical rangefinder. Along the open coast, Loran C readings were recorded at points we estimated the trawl first contacted and left bottom and were later converted to distance fished.

We sorted most of the catch by species (some fishes to family only), and information was recorded for total weight and number per haul. Random subsampling of the catch (never <20% by weight) was performed when necessary to speed processing. Length frequencies and individual lengths and weights were recorded for selected species.

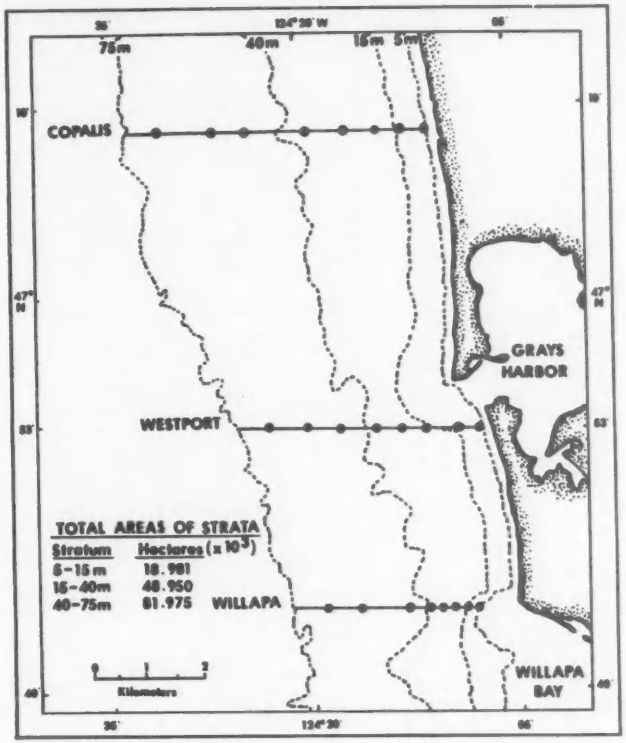

FIGURE 2.—Chart of the open coast adjacent to Grays Harbor, WA, showing the isobaths, tracklines, and systematic trawl stations.

Data Analyses

Nautical charts of Grays Harbor and the adjacent open coast were digitized and strata areas were calculated (Figs. 1, 2), using computerized algorithms available in the software library of the NWAFC Resource Assessment and Conservation Engineering Division. Strata were defined for the offshore area by first extending the north and south boundaries 5 nmi from the Copalis and Willapa transects, respectively, and then determining the area between the 5, 15, 40, and 75 m depth contours.

Estimates of mean density of young English sole by stratum by month, population by stratum, and total population for each survey area were calculated, using slight modifications of the methods of Pereyra et al. (1976). In calculating density estimates (number/hectare) from catch per kilometer, the efficiency coefficient of the gear was assumed to be unity (i.e., all fishes in the path would be captured). Length frequencies for 5 mm (TL) size intervals were used to calculate size composition. Age classes were then determined by visual inspection of the resultant length-frequency histograms. Afterwards, the proportion of individuals within the size range of the 0-age group in a particular month was multiplied by the total population for that month to provide an estimate of the abundance of 0-age recruits.

Results

Over the course of the 2-yr study, we completed a total of 592 trawls, 349 within Grays Harbor and 243 along the open coast (Table 1). Hauls within the

TABLE 1.—Allocation of sampling effort indicating the number of successful trawls completed for each trip.

Survey area	1983			1984		
	Month	Trips	Trawls	Month	Trips	Trawls
Estuary	Apr.	2	9,13	Jan.	1	13
	May	2	13,16	Apr.	1	5
	June	2	16,14	May	2	15,16
	July	2	16,16	June	2	18,18
	Aug.	2	14,16	July	2	18,17
	Sept.	1	16	Aug.	2	19,17
	Oct.	1	16	Sept.	1	18
Total			175			174
Open coast	May	1	17	Apr.	1	19
	July	1	20	May	1	23
	Aug.	1	25	June	1	26
	Sept.	1	48	Aug.	1	32
				Sept.	1	33
Total			110			133

estuary averaged 0.25 km at 2.52 km/h, while in the coastal study area they averaged 0.91 km at 3.32 km/h.

Distribution and Abundance

We captured a total of 13 species of flatfishes in the two study areas during the 2-yr survey (Table 2). Juvenile sanddab, sand sole, and English sole were found to be abundant both in Grays Harbor estuary and along the open coast. Two species in particular, English sole and starry flounder, were found to have much higher densities in the estuary than along the open coast (Table 2). English sole were found to be the most abundant flatfish in the estuary for both years and along the open coast in 1984.

For both years within Grays Harbor, densities of English sole generally were highest in STR 1, 2, and 4 and lowest densities in STR 3 (Table 3). Apart from changes due to recruitment, fluctuation in abundance in the four areas of the estuary was likely affected by movement of juveniles between strata and between the estuary and open coast. Along the open coast, greatest densities were observed nearshore (Table 4) in depths <40 m. In 1984, English sole were most abundant at 5–15 m owing to the presence of high numbers of 0-age fish.

Mean density (all months combined) within the estuary was over 20 times greater than the open coast in 1983. Settlement of fish <25 mm TL was much greater in 1984 than 1983 in both areas, but estuarine density was still higher than that of the open coast. A t-test was performed on log-transformed CPUE (Zar 1984) because catch data are typically nonnormally distributed. Results showed a significantly greater density ($P < 0.0001$) of juvenile English sole in the estuary than along the open coast for both 1983 (562 vs. 23 mean no./ha) and 1984 (1,149 vs. 178 mean no./ha).

Population Estimates

In making population estimates, mean densities of fish less than age V by month were multiplied by strata areas. Comparison of length frequencies of fish we collected with published age-at-length relationships (Van Cleve and El Sayed 1969) indicated that fish beyond age IV were rarely captured. Older fish may not have been present in the study areas

TABLE 2.—Stratified mean densities and 2 SE (in parentheses) for juvenile flatfish captured in the two survey areas for 1983–84.

Species	1983 densities (no./ha)		1984 densities (no./ha)	
	Estuary	Open coast	Estuary	Open coast
English sole, *Parophrys vetulus*	562(132)	23(10)	1,149(237)	178(101)
Pac. Sanddab, *Citharichthys sordidus*	147(30)	94(24)	94(33)	65(22)
Butter sole, *Isopesetta isolepsis*	<1	37(10)	<1	13(4)
Sand sole, *Psettichthys melanosticus*	27(11)	10(6)	36(14)	23(11)
Dover sole, *Microstomus pacificus*	—	11(5)	—	8(4)
Rex sole, *Glyptocephalus zachirus*	—	10(5)	—	2(2)
Slender sole, *Lyopsetta exilis*	—	2	—	1
Starry flounder, *Platichthys stellatus*	25(16)	<1	10(7)	1
Petrale sole, *Eopsetta jordani*	—	<1	—	<1
Rock sole, *Lepidopsetta bilineata*	—	<1	—	<1
C-O sole, *Pleuronichthys coenosus*	<1	<1	—	—
Curlfin sole, *Pleuronichthys coenosus*	<1	<1	—	<1
Cal. tonguefish,[1] *Symphurus atricauda*	<1	<1	—	—

[1]Occurrence considered anomolous (Dinnel and Rogers 1986).

TABLE 3.—Population estimates for juvenile English sole in the estuary survey area by date (month/year) and by stratum (1–4). The 95% confidence interval for the total population is obtained by adding or substracting the value in parentheses.

Date	Stratum	Density (no./ha)	Population (millions)	Date	Stratum	Density (no./ha)	Population (millions)
4/83	1	82	0.301	1/84	1	66	0.239
	2	127	0.318		2	100	0.251
	3	312	0.483		3	207	0.320
	4	383	0.318		4	158	0.131
	Total		1.421 (0.851)		Total		0.942 (0.472)
5/83	1	1,138	4.154	5/84	1	2,191	7.999
	2	297	0.747		2	4,858	12.223
	3	84	0.130		3	575	0.890
	4	1,825	1.515		4	2,045	1.697
	Total		6.545 (5.045)		Total		22.808 (8.686)
6/83	1	681	2.488	6/84	1	1,092	3.986
	2	961	2.417		2	1,049	2.639
	3	71	0.110		3	160	0.248
	4	801	0.665		4	835	0.693
	Total		5.679 (3.089)		Total		7.565 (4.195)
7/83	1	717	2.616	7/84	1	1,360	4.966
	2	775	1.950		2	2,470	6.214
	3	222	0.344		3	212	0.328
	4	740	0.614		4	1,087	0.902
	Total		5.524 (3.836)		Total		12.411 (5.569)
8/83	1	648	2.365	8/84	1	1,285	4.691
	2	662	1.666		2	939	2.362
	3	390	0.604		3	417	0.645
	4	468	0.388		4	402	0.333
	Total		5.023 (2.898)		Total		8.031 (3.557)
9/83	1	765	2.793	9/84	1	124	0.451
	2	291	0.733		2	558	1.403
	3	195	0.301		3	755	1.169
	4	524	0.435		4	262	0.217
	Total		4.262 (2.772)		Total		3.241 (1.745)
10/83	1	125	0.457				
	2	598	1.505				
	3	564	0.873				
	4	115	0.095				
	Total		2.931 (1.251)				

or, more likely, were better able to avoid the narrow beam trawl.

Within the estuary, English sole were most numerous in May of both years, but the peak of 22.8 million in 1984 was more than 3 times higher than the peak of 6.5 million in 1983 (Table 3). Although the distribution of the English sole population within the estuary was highly variable, the bulk of the population was in STR 1 or STR 2 for most months. Along the open coast, the English sole population peaked at the same time and at generally the same levels as the estuary for both years, about 5.9 and 23.2 million for 1983 and 1984, respectively (Table 4). Comparable populations of young fish occurred in both areas despite the 18 times greater geographic extent of the offshore survey area.

Recruitment

Relative recruitment to the two survey areas was measured in terms of populations of 0-age fish. Within the estuarine study area, recently transformed (<25 mm TL; Laroche et al. 1982) English sole were observed from April to July in 1983, and in January and from May to August in 1984. Peak abundance of this size range was observed in May of both years, but it is highly likely that early spring peaks were missed since our study lacked adequate coverage of fall, winter, and early spring months. Duration of settlement along the Oregon coast is known to be much longer than observed in our study (Laroche and Richardson 1979; Boehlert and Mundy 1987). Along the open coast, settlement seemed to

TABLE 4.—Population estimates for juvenile English sole in the open coast survey area by date (month/year) and by stratum (1–4). The 95% confidence interval for total population is obtained by adding or substracting the value in parentheses.

Date	Depth (m)	Density (no./ha)	Population (millions)	Date	Depth (m)	Density (no./ha)	Population (millions)
5/83	5–15	6	0.115	4/84	5–15	165	3.124
	15–40	100	4.881		15–40	47	2.318
	40–75	11	0.887		40–75	55	4.525
	Total		5.883 (4.666)		Total		9.967 (7.071)
7/83	5–15	2	0.044	5/84	5–15	190	3.598
	15–40	20	0.983		15–40	80	3.911
	40–75	8	0.680		40–75	191	15.667
	Total		1.707 (1.840)		Total		23.176 (19.225)
8/83	5–15	54	1.028	6/84	5–15	226	4.282
	15–40	35	1.709		15–40	48	2.356
	40–75	12	0.991		40–75	9	0.732
	Total		3.728 (2.390)		Total		7.370 (3.110)
9/83	5–15	12	0.230	8/84	5–15	903	17.133
	15–40	32	1.547		15–40	14	0.670
	40–75	3	0.269		40–75	21	1.724
	Total		2.045 (0.902)		Total		19.527 (18.981)
				9/84	5–15	97	1.836
					15–40	322	15.761
					40–75	5	0.402
					Total		18.000 (11.494)

be of shorter duration, though again, the survey lacked sampling effort from October through March. Recently transformed juveniles were captured only during May in 1983 and were found from April to September in 1984. Peak abundance was observed in May as in the estuary.

Populations of 0-age fish were determined using estimates of total juvenile population (Tables 3, 4) and size-frequency data (Table 5). These estimates show that English sole had higher recruitment to the estuary than to the open coast for early spring of both years. The estuarine population of young-of-the-year exceeded that of the open coast by over four times (6.4 vs. 1.5 million) in May 1983. The difference was less pronounced in May 1984, but the estuarine population was again higher (22.8 vs. 19.0 million). Later in summer in both years, the estuarine population of 0-age fish declined to a greater extent than that along the open coast, but some of the relative change is likely due to emigration from the estuary.

Densities were plotted by 5 mm length interval for the estuarine and open coast study areas for May each year, a period of high settlement (Fig. 3). Densities of juveniles <25 mm were more than 10 times greater in the estuary, indicating disporportionately higher direct settlement and/or higher mortality of newly settled juveniles in the open coast area. When

TABLE 5.—Length ranges (mm TL) of 0-age English sole determined from visual inspection of length-frequency distributions by study area and by date (month/year). Modal and mean lengths, and the proportion of total population comprised by the 0-age group are also indicated.

Study area	Date	Range (mm)	Mode (mm)	Mean (mm)	Proportion
Estuary	4/83	19– 84	65	57.6	0.85
	5/83	19– 99	30	50.5	0.97
	6/83	18–114	40	62.5	0.98
	7/83	26–119	55	73.8	0.99
	8/83	43–124	70	79.1	0.99
	9/83	49–145	80	87.0	1.00
	10/83	62–130	85	92.8	1.00
	1/84	25– 54	35	34.9	0.58
	5/84	15– 84	20	26.9	1.00
	6/84	20– 99	30	46.4	0.96
	7/84	25–114	85	66.9	0.99
	8/84	30–124	90	84.8	0.99
	9/84	50–135	90	92.0	1.00
Open coast	5/83	21– 60	35	33.3	0.25
	7/83	99–115	100	104.0	0.07
	8/83	43–165	120	115.4	0.80
	9/83	53–200	110	134.7	0.89
	4/84	15– 35	20	19.5	0.90
	5/84	15– 90	20	26.5	0.82
	6/84	15–120	30	48.6	0.87
	8/84	20–160	95	91.0	0.98
	9/84	20–180	130	119.0	0.89

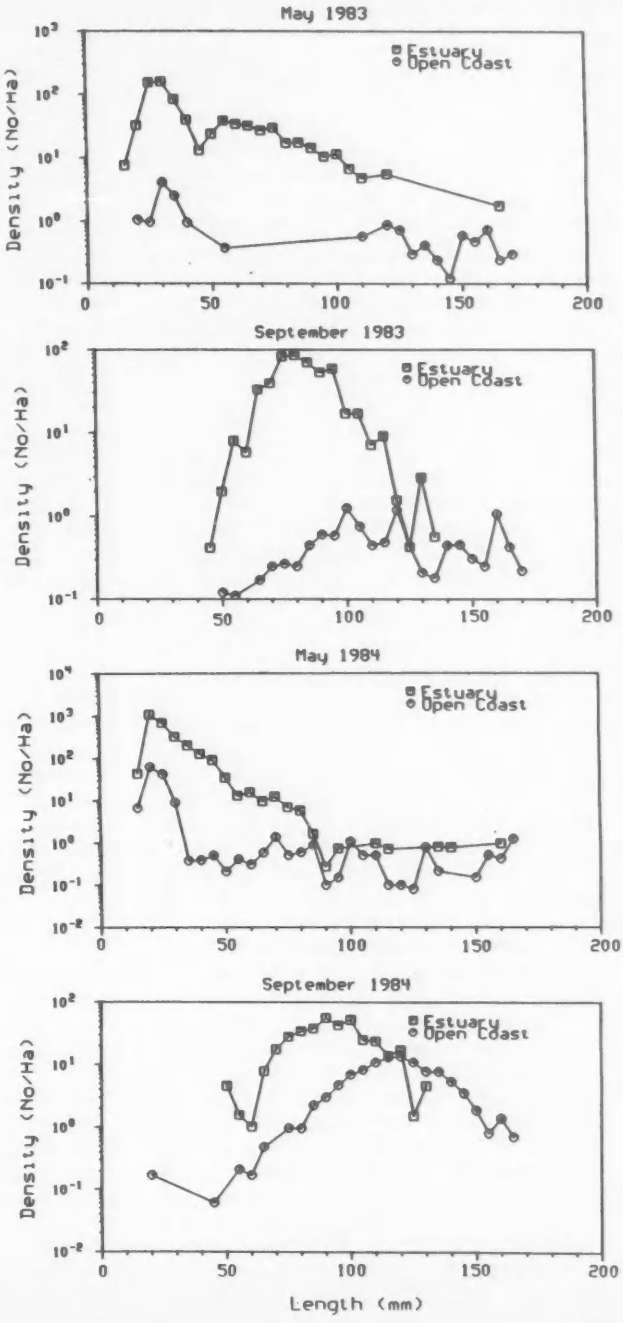

FIGURE 3.—Density of juvenile English sole by length interval for May and September of 1983 and 1984. Note the higher density of 0-age fish in the estuary each spring.

densities were plotted by length interval the following September of each year, it was evident that fish over 140 mm were not available in the estuary and had probably emigrated to the open coast.

Discussion

If there is an adaptive advantage in utilizing estuarine nursery grounds rather than the open coast, there must exist a mechanism for 0-age fish to enter estuarine systems. Although English sole larvae are abundant in coastal waters (Richardson and Pearcy 1977), early stages have not been prevalent in estuarine larval surveys (Pearcy and Meyers 1974; Misitano 1977). Large transforming larvae (18–23 mm) have been collected in Humboldt Bay and Columbia River estuary (Misitano 1976, 1977), and in Yaquina Bay (Boehlert and Mundy 1987). Immigration of 0-age English sole to the Grays Harbor estuary may be accomplished by direct settlement of transforming larvae after simple advection by ocean water into the bay, or by movements of newly settled benthic juveniles. Such movement could be accomplished either actively or by selective tidal transport as noted for juvenile flatfishes in the North Sea (DeVeen 1978).

During the period of this study, newly transformed English sole were found both within the Grays Harbor estuary and along the adjacent open coast. English sole have also been shown to enter Yaquina Bay after settlement (Boehlert and Mundy 1987) so it is likely that both transforming larvae and settled juvenile English sole may enter Grays Harbor. Krygier and Pearcy (1986) found newly transformed English sole to be more abundant in open coastal areas and presumed movement into Oregon estuaries to occur predominantly after transformation. The occurrence of recently transformed benthic juveniles in such high numbers throughout Grays Harbor suggests direct settlement of late stage larvae after advection into the estuary may also be an important mode of entry.

Emigration of the largest fish to the open coast took place during late summer, and all fish larger than 140 mm were found exclusively in the open coast area by September. Studies of other estuarine nursery areas have indicated that the emigration process involves the larger size classes of 0-age fish (Herke 1971; Weinstein 1983). Emigration from Yaquina Bay of the larger 0-age English sole has been noted in the fall (Westrheim 1955; Olsen and Pratt 1973; Bayer 1981). Angell et al. (1975) observed a similar phenomenon for young English sole in a Puget Sound nursery area.

The departure of larger juveniles later in summer may be in response to changing environmental conditions and may be indicative of the limits of the carrying capacity of estuaries being exceeded for populations of juvenile fish (Krygier and Pearcy 1986). Alternatively, a change in dietary preferences of larger 0-age fish may cause them to leave estuaries in search of prey items (Toole 1980), thus reducing intraspecific competition. The advantage in utilization of estuarine nurseries then, may be more for protection of vulnerable sizes rather than for accelerated growth (Rosenberg 1982).

Even though our study found a great deal of interannual variability, the Grays Harbor estuary and other nearby estuaries (Shi 1987) clearly are important nursery grounds for juvenile English sole, which had similar size populations in the estuarine and offshore study areas despite the greater geographic extent of the latter. Peak population estimates for 0-age English sole for the month of May show that 81% and 54% of 0-age fish in the Grays Harbor area were found in the estuary in 1983 and 1984, respectively. This is probably an underestimate of the degree of estuarine dependence, however, because some juveniles may move into the estuary later in the summer. Nevertheless, our results show that at least half of the 0-age English sole in the Grays Harbor nearshore area make use of an estuary during the first year of life. This kind of information will prove useful in assessing the economic impact on commercial fisheries from navigation and industrial development projects, which may contribute to habitat degradation in Grays Harbor.

Acknowledgments

This note represents part of a Masters Thesis submitted to the University of Washington School of Fisheries by C. W. Rogers. Work was supported primarily by the Washington Sea Grant Program (NOAA grant NA81AA-D00030, R/F-49). Data processing assistance from the Northwest and Alaska Fisheries Center is gratefully acknowledged. Logistic support was provided by the U.S. Coast Guard and the Washington Department of Fisheries. The senior author also acknowledges the sponsors of the Melvin G. Anderson Memorial Scholarship and the Graduate School of the University of Washington for support of portions of this work. We are gratefully indebted to all who assisted in field collections,

especially D. Samuelson, K. Carrasco, A. R. Black, and B. Gutermuth.

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LENGTH-WEIGHT RELATIONSHIPS FOR GULF FLOUNDER, *PARALICHTHYS ALBIGUTTA*, FROM NORTH CAROLINA

Ginsburg (1952) resolved that the gulf flounder, *Paralichthys albigutta*, ranging from North Carolina to Laguna Madre, TX (Topp and Hoff 1972; Hoese and Moore 1977; Robins and Ray 1986), was a *Paralichthys*. Topp and Hoff (1972) summarized the many distributional records known throughout its range. Other than keys to the species of *Paralichthys* (Gutherz 1967), much of the biology of the gulf flounder remains unknown even though it abounds east of the Mobile Bay system (Joseph and Yerger 1956; Topp and Hoff, 1972; Shipp 1986).

Some researchers cite a 390 mm (total length, TL) Cedar Key, FL specimen (Jordan and Swain 1885) as the largest size attained by the gulf flounder (Hoese and Moore 1977; Robins et al. 1986). Vick (1964) noted a 710 mm, 5 kg, specimen in the sport fishery off Panama City, FL but did not furnish data on specimens larger than 380 mm TL.

We present length-weight regression data for North Carolina gulf flounder from 263 to 673 mm TL and 318 to 3,706 g.

Methods

Since 1975, 75 gulf flounder were speared while scuba diving along the Cape Lookout rock jetty (13 km east) and the artificial fishing reef (3 km SE) off Morehead City, NC. Most dives occurred in November and December, when *P. albigutta* and other paralichthids congregated in nearshore ocean waters off Carteret County, NC prior to their offshore spawning migration. Specimens were weighed to the nearest gram on beam balances and measured (total length) in millimeters within hours of capture.

Observations

While gulf flounder are not abundant in North Carolina (Schwartz et al. 1979, 1982), they are captured by hook and line or spear fishermen when the fish frequent high saline nearshore ocean waters or inlets (Schwartz 1979, 1982). Species of *Paralichthys* can usually be separated from each other by the number of gill rakers on the lower first gill arch, fin ray count, spotting, body width, salinity preference, and depth distribution preference (Gutherz 1967). Gulf flounder possess 9–12 (usually 10–11) gill rakers on the lower first arch, 53–63 anal rays, and three prominent ocellated spots arranged in a triangular pattern. North Carolina gulf flounder had 9–13 gill rakers on the lower first arch (65 specimens) and 54–67 anal fin rays. Complete anal rays were not counted in 17 specimens.

Gulf flounders caught consisted of 13 males and 62 females. Males ranged from 310 to 426 mm TL

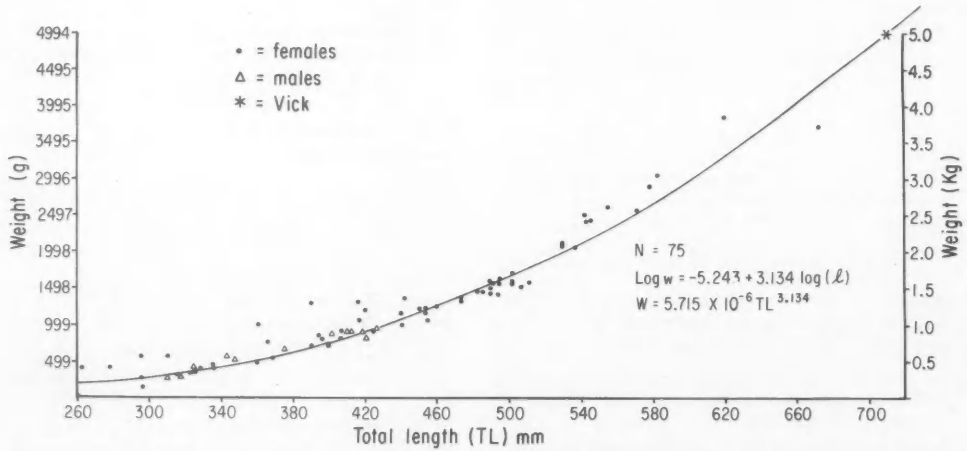

FIGURE 1.—Length-weight relationship for gulf flounders, *Paralichythys albigutta*, from North Carolina. Asterisk represents Vick's specimen.

and weighed 318 to 949 g, while females ranged from 263 to 673 mm TL and 408 to 3,706 g (Fig. 1). The length-weight relationship for North Carolina gulf flounder can best be expressed as $\log w = -5.24 + 3.134 \log l$ for 75 specimens (sexes combined), $r = 0.957$ (Fig. 1). Little change occurred when the male data was removed because the female length-weight relationship was virtually the same: $\log w = -5.018 + 3.053 \log l$ ($N = 62$), $r = 0.955$. Vick's (1964) large specimen, 710 mm TL, 5,000 g, fits right on our regression curve. Thus, there is little doubt that his specimen was *P. albigutta* because *P. dentatus* does not occur in the Gulf of Mexico (Robins and Ray 1986), and *P. squamilentus* or *P. lethostigma* possess other distinguishing meristic, morphometric, and ecological requirements (Vick 1964; Gutherz 1967).

The maximum known upper size and weight can now be raised to at least 673 mm and 3,706 g in North Carolina.

Acknowledgments

Thanks are extended to the North Carolina Marine Reef program personnel, which included G.W.S., for assisting in collecting flounders in 1975. Val and Henry Page produced Figure 1; Charleen Miller, Texas A&M Research Foundation, was instrumental in locating Vick's 1964 report; and Brenda Bright typed the manuscript.

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FUNCTIONAL REGRESSION EQUATIONS FOR ZOOPLANKTON DISPLACEMENT VOLUME, WET WEIGHT, DRY WEIGHT, AND CARBON: A CORRECTION

The objective of this note is to point out the fact that the first nine equations published by Wiebe et al. (1975, table 2) were those appropriate for the Y on X regressions; they were not the functional regression equations as originally claimed. This mistake was discovered as a result of correspondence with F. A. Ascioti (Dip. di Biologia Animale Ed Ecologia Marina; Universita di Messina; Via Dei Verdi 75; 98100 Messina ITALY). This table 2 should have had the following equations in it:

Equation	*Regression equation*	*N*
1	$LOG(DV) = -1.434 + 0.820\ LOG(C)$	87
2	$LOG(WW) = -1.537 + 0.852\ LOG(C)$	70
3	$LOG(DW) = 0.499 + 0.991\ LOG(C)$	195
4	$LOG(DV) = -1.842 + 0.865\ LOG(DW)$	163
5	$LOG(WW) = -2.002 + 0.950\ LOG(DW)$	95
6	$LOG(DV) = 0.139 + 1.003\ LOG(WW)$	77
7	$LOG(BWW) = -1.947 + 1.050\ LOG(BDW)$	421
8	$LOG(BDV) = -1.887 + 1.007\ LOG(BDW)$	404
9	$LOG(BDV) = 0.005 + 0.981\ LOG(BWW)$	403

10	LOG(PDW)	=	0.853 + 1.024	LOG(PC)	45
11	LOG(DV)	=	1.037 + 0.839	LOG(DW)	111
12	LOG(WW)	=	0.975 + 0.946	LOG(DW)	94
13	LOG(DV)	=	0.107 + 1.082	LOG(WW)	76

To prepare these GM functional regression equations (Ricker 1973:412), the original data were checked and log transformed, and the regressions recomputed. The variances and correlation coefficients remain essentially unchanged. Note that in Wiebe et al. (1975) and above, equations 1–10 are based on biomass standardized to per cubic meter while the remainder are not. Equations 6 and 10 in table 2 of Wiebe et al. (1975) also contained errors; the intercept of equation 6 was incorrectly printed as 0.670 rather than 0.067; the intercept of equation 10, which was 0.558, has been corrected to 0.853.

The equations listed above, when compared with those originally presented, provide estimates of x given y or y given x, which generally differ by less than 6% in the central part of the data set and by less than 15% in the tails of the data set. Samples similar in biomass and taxonomic composition to those used in this study, which we have analyzed for size of individuals as a function of taxonomic unit (Davis and Wiebe 1985), contain animals which typically range in size from 0.35 mm to 100 mm.

For a number of samples for which we reported carbon values, nitrogen values were also obtained from the CHN analyzers we used (Table 1, this note). Although carbon to nitrogen conversion factors exist in the literature, few are based on data ranging over as many hydrographic regimes as does data presented in Wiebe et al. (1975). Since a growing number of mathematical models use nitrogen rather than carbon as the basic currency, we take this opportunity to present these data (Fig. 1) and the resulting carbon/nitrogen ratio.

Functional regression of carbon versus nitrogen yielded the following significant ($P < 0.01$; $r^2 = 0.99$) relationship:

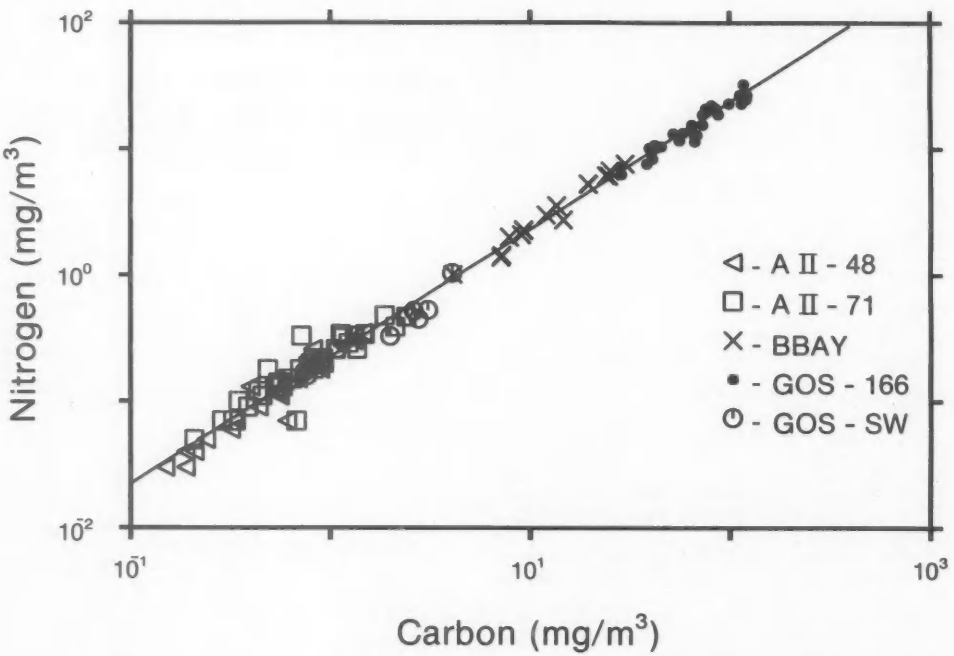

FIGURE 1.—Plot of data used in calculating the regression relating carbon and nitrogen in zooplankton collections from areas specified in Table 1.

TABLE 1.—Number of zooplankton samples for each cruise from which both carbon and nitrogen were measured. The general location of the stations for these samples are given in Wiebe et al. (1975).

Cruise or area	Date	No. of measurements	Diameter of net (mesh size)
Buzzards Bay	Jan.–June 1972	16	70 cm (240 μm)
Slope Water (RV *Gosnold*)	June–Aug. 1972	12	100 cm (333 μm)
Atlantis II 48 (Gulf of Mexico)	Nov. 1968	19	70 cm (240 μm)
Gosnold 166 (New York Bight)	June 1970	33	70 cm (240 μm)
Atlantis II 71 (Sargasso Sea)	Sept. 1972	39	100 cm (333 μm)

$$\text{Nitrogen (mg/m}^3) = -0.0247 + 0.2324 \text{ carbon (mg/m}^3)$$

Essentially the carbon/nitrogen ratio of the bulk zooplankton we collected is a constant (4.30) over a broad range of values and oceanographic habitats. As an atomic ratio, 5.02, this value is lower than that predicted by the Redfield ratio, 6.63 (Redfield et al. 1963), an indication that zooplankton are nitrogen rich relative to their phytoplankton counterparts.

Acknowledgments

We would like to express our appreciation to F. A. Ascioti for his correspondence and attention to detail which enabled us to correct the mistakes in our previous publication. This research was supported by NSF Grant OCE-8709962 and is Contribution No. 6839 from the Woods Hole Oceanographic Institution.

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ELECTROPHORETIC IDENTIFICATION OF EARLY JUVENILE YELLOWFIN TUNA, *THUNNUS ALBACARES*

Early juveniles, 13 mm standard length (SL) or larger, of yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*, cannot be distinguished on the basis of meristic, morphological, or pigmentation characters (Matsumoto et al. 1972). Collette et al. (1984) reported that most species of the genus *Thunnus* can be distinguished at the larval stage by melanophore patterns. Matsumoto et al. (1972) and Nishikawa and Rimmer (1987) suggested that *T. albacares* and *T. obesus* larvae can be separated by the respective absence or presence of postanal ventral melanophores. Confirmation of the identification of *T. albacares* larvae has been obtained through laboratory rearing studies (Harada et al. 1971; Mori et al. 1971). However, the use of postanal ventral pigmentation patterns as reliable characters to distinguish yellowfin and bigeye tuna larvae has been questioned by Richards and Pothoff (1974). Nishikawa and Rimmer (1987) stated that it is virtually impossible to identify to species the early juvenile stages, 15 to 60 mm SL, of *Thunnus* because larval pigmentation patterns become obscured and are no longer diagnostic. Furthermore, Pothoff (1974) was unable to separate *T. albacares* and *T. obesus* as early juveniles, 8 to 100 mm SL, on the basis of osteological characters.

Electrophoresis of water soluble proteins has been used to distinguish morphologically similar larval and early juvenile marine fishes (Morgan 1975; Smith and Crossland 1977; Sidell et al. 1978; Smith and Benson 1980). Sharp and Pirages (1978) presented starch gel electrophoretic patterns for several loci of adults of many scombrid species, including most members of the genus *Thunnus*. Although electrophoretically very similar, adults of yellowfin and bigeye tuna can be unambiguously distinguished by the electrophoretic pattern of the muscle isozyme of glycerol-3-phosphate dehydrog-

enase (alpha glycerol phosphate). This locus has been used to identify adults of the genus *Thunnus* in the absence of complete morphological data (Dotson and Graves 1984). This paper describes an application of the above techniques, modified for work with small tissue samples, to the identification of an opportunistic collection of early juvenile tuna, in excellent morphological condition, which were frozen shortly after capture. The early juveniles in this collection encompassed the pigmentation patterns reported for both *T. albacares* and *T. obesus*.

Specimens were collected aboard the MV *Royal Polaris*, a San Diego-based sportfishing boat, about 1 km off Clipperton Island in the eastern Pacific (lat. 10°23′N, long. 109°15′W), 8 May 1986, from hours of 2100 to 2400. The early juveniles were caught underneath floodlights at a depth of about 1 m with a fine (1 mm) mesh, long-handled dip net. They were not present at the surface. After each pass, the dip net contents were sorted for scombrid larvae. Approximately 100 specimens were collected, most of which were quickly frozen in seawater.

Adult specimens of *T. albacares* and *T. obesus* were collected by hook and line off the Pacific coast of southern and northern Baja California, Mexico, respectively. White muscle tissue samples were removed from freshly caught specimens and quickly frozen.

The early juveniles collected off Clipperton Island were thawed in the laboratory and examined under a dissecting microscope. Those juveniles positively identified to the morphologically indistinguishable *T. albacares*/*T. obesus* complex were measured for total length (TL) to the nearest millimeter and examined for postanal ventral pigmentation pattern. Heads were removed and placed in 95% ethanol for otolith studies. The remaining trunk and tail musculature was placed in a small (1.0 mL) microfuge tube, and 60 μL of cold grinding buffer (0.1 M Tris, pH 7.5) was quickly added. Tissues were homogenized with a cold ground-glass rod contoured to fit snugly within the microfuge tube. Approximately 10 seconds of rod rotation were required to completely disrupt the tissues. The homogenate was centrifuged for 2 minutes in a microfuge and stored on ice until electrophoresis.

Two grams of adult tissue were disrupted for approximately 20 seconds in 4 volumes of cold grinding buffer in a motor-driven, ground-glass tissue homogenizer. The homogenate was centrifuged at 5,000 *g*, 4°C, for 10 minutes. The supernatant was removed, diluted 10:1 with cold grinding buffer, and stored on ice until electrophoresis.

Horizontal starch gel electrophoresis was performed on 12% (W/V) gels run in the Tris/Citrate II system of Selander et al. (1971). Gels were run at 45 to 50 mA for 3.5 hours. Glycerol-3-phosphate dehydrogenase was stained using the protocol of Shaw and Prasad (1970). Three sets of standards composed of the supernatants of muscle tissue homogenates of adult yellowfin and bigeye tuna were placed in each gel to score the early juveniles.

A total of 77 early juveniles, ranging in length from 10 to 21 mm TL, were processed. Glycerol-3-phosphate dehydrogenase activity was scored for 68 individuals. All early juveniles displayed a muscle-type glycerol-3-phosphate dehydrogenase band of low anodal mobility, identical to that of the yellowfin tuna adults (Fig. 1). No individuals with the faster migrating *T. obesus* glycerol-3-phosphate dehydrogenase band were detected.

The lack of bigeye tuna juveniles in this study could be the result of two possibilities: either the early juveniles were all yellowfin tuna or both yellowfin and bigeye tuna early juveniles share a muscle-type glycerol-3-phosphate dehydrogenase isozyme of similar electrophoretic mobility. However, differential ontogenetic expression of electrophoretically distinct isozymes has not been reported for fishes in studies that have used adult allozymes to identify larvae or early juveniles (Morgan 1975; Smith and Crossland 1977; Sidell et al. 1978; Smith and Benson 1980) or in investigations of ontogenetic expression of electrophoretic loci (Shaklee et al. 1974; Siebenaller 1984). Thus, the electrophoretic similarity of the glyceraldehyde-3-phosphate alleles of the early juveniles investigated in this study most likely indicates that they were all yellowfin tuna.

On the same trip during which the early juveniles were collected at Clipperton Island, about 300 adult yellowfin tuna were caught on hook and line but no bigeye tuna were taken. Histological examination of ovarian tissue from several of the adult yellowfin tuna revealed postovulatory follicles, indicating that spawning was taking place (Anonymous 1987). On the basis of this information, it is not unexpected that all the early juveniles identified electrophoretically in this study proved to be *T. albacares*.

A wide range of postanal ventral pigmentation patterns (red and black) was displayed by the early juveniles. Since these specimens were collected at night, the pigment cells, when present, were distinct and brightly colored as reported by Matsumoto et al. (1972). While some individuals had no melanophores in this region, others had from one to eight.

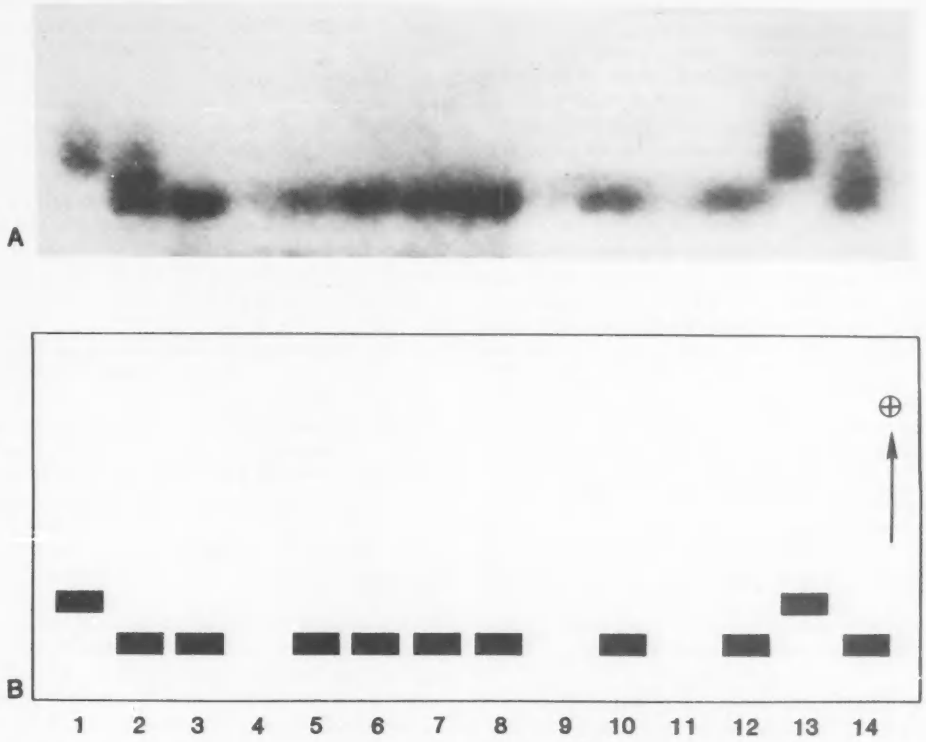

FIGURE 1.—Photograph (A) and line drawing (B) of a gel demonstrating electrophoretic mobilities of muscle-type glycerol-3-phosphate dehydrogenase alleles of yellowfin and bigeye tuna. Bigeye tuna display an allele with a greater anodal mobility. The gel includes adult bigeye (lanes 1 and 13) and yellowfin (lanes 2 and 14) tuna standards and 7 early juveniles, all identified as yellowfin tuna. Note that three individuals (lanes 4, 9, and 11) did not have sufficient activity to stain.

According to Matsumoto et al. (1972) and Nishikawa and Rimmer (1987), yellowfin larvae less than about 12 mm SL have no black pigment spots in the ventral tail region. However, Mori et al. (1971) reported and illustrated that there is black pigmentation on the ventral edges of the tail in laboratory-reared yellowfin larvae at 7.8 mm TL. Twenty-one individuals in the 10 to 12 mm TL size range were electrophoretically typed as yellowfin tuna in this study. Six of these early juveniles had black postanal ventral pigmentation (characteristic of bigeye tuna), while 15 had no black postanal ventral pigmentation (characteristic of yellowfin tuna).

Variability in larval and early juvenile pigmentation within species, including large changes in pigmentation over small size ranges, is found within many marine fishes (Powles and Markle 1984). Richards and Pothoff (1974) have suggested that the variability of postanal ventral pigmentation is not consistent with specific differentiation within the *T. albacares*/*T. obesus* complex. This study supports their claim.

Early life history studies are necessary for an understanding of recruitment within each species of tuna. Due to the morphological similarity of yellowfin and bigeye tuna larvae and early juveniles, specific separation has not been possible. This study provides a simple method for identifying yellowfin and bigeye tuna larvae and early juveniles. With this technique and additional material, it may be possible to find a morphological character that will allow rapid identification of these two species.

Acknowledgments

We would like to thank the owner, Frank LoPreste, and skipper, Steve Loomis, as well as the crew of the MV *Royal Polaris* for providing the opportunity to collect specimens. William H. Bayliff and Witold L. Klawe reviewed the manuscript.

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A COMPARISON OF DEMERSAL ZOOPLANKTON COLLECTED AT ALLIGATOR REEF, FLORIDA, USING EMERGENCE AND REENTRY TRAPS

Demersal zooplankton have been shown to be important components of a number of marine communities, including coral reefs (Porter and Porter 1977; Alldredge and King 1977), kelp beds (Hammer 1981), and other habitats (Thomas and Jelley 1972). They probably play an important role in the flux of particulate material through benthic communities (Porter and Porter 1977). Demersal zooplankton can also be important prey for fish and other consumers (Alldredge and King 1977, 1980).

Demersal zooplankton are usually sampled by techniques that take advantage of their migration into or out of the plankton. Studies by Alldredge and King (1980, 1985) and Youngbluth (1982) suggest

that sampling methods used to collect demersal zooplankton can have a significant effect on the numbers and kinds of animals collected. The most widely used method to date is emergence trapping, in which zooplankton are collected as they migrate out of the substrate, e.g., Porter and Porter (1977). Another method, reentry trapping, captures zooplankton as they enter the substrate, e.g., Alldredge and King (1980). A primary purpose of this study was to compare results from simultaneous emergence and reentry trapping, and verify Alldredge and King's (1980) finding that reentry traps capture significantly more zooplankton than emergence traps.

Horizontal currents are likely to have major but variable effects on the transport of demersal organisms in the plankton. Organisms migrating high into the water column are likely to be transported laterally to a greater extent than those that remain in the near-bottom layer, as Alldredge and King (1985) have suggested. Thus, the implicit assumption of some other investigators that demersal zooplankton are characteristic residents of a habitat needs qualification. Horizontal transport of migrating demersal zooplankton is probably an important recruitment mechanism and a means by which planktivorous fish associated with reefs and other structures are supported. Demersal zooplankton have been shown to be associated with sand bottoms by Alldredge and King (1977, 1980), so sand bottoms might be an important source of demersal zooplankton for reef communities. Therefore, our purpose in this study was also to assess the abundance of demersal zooplankton on sand bottom habitat. The study addressed the questions: how abundant are different taxa of demersal zooplankton associated with sand bottom habitat? Can different trapping techniques distinguish zooplankters with different propensities for horizontal transport by currents? How do the abundance and taxonomic composition of demersal zooplankton on open carbonate sand compare with the finding of others studying similar sand bottoms?

Materials and Methods

Study sites were located approximately 1.8 km east of Alligator Reef Buoy, ca. 7.5 km southeast of Upper Matecumbe Key in the Florida Keys (lat. 24°41.26′N, long. 80°35.68′W). The sites were characterized by a subtidal, carbonate sand bottom that sloped gently from depths of 2–4 m to depths of over 40 m. Macrophytes occurred sparsely on the bottom (principally *Thalassia* sp.), with the closest coral structure and associated fish populations several hundred meters downstream. Currents were minimal (<0.05 m s^{-1}) and flowed to the northeast, parallel to the axis of the Gulf Stream just offshore.

Sampling at the site was conducted with the aid of scuba, supported by the NOAA-National Undersea Research Program's RV *Seahawk*, which operated in the Florida Keys region during March 1985.

Demersal zooplankton were sampled simultaneously by emergence trapping and reentry trapping. The emergence traps were a simplified version of those used by Hobson and Chess (1979), consisting of a single cone of 95 μm mesh netting 1 m high and 21 cm diameter at the mouth (Fig. 1). The mouth of the net was weighted with lead weights sewn into the mouth collar to aid placement on the bottom. A 1 L polyethylene bottle with a polyethylene funnel in the throat was attached to the upper end of the net; the bottles' natural buoyancy extended the traps. Reentry traps were square polyethylene pans, 21 cm per side and 5 cm deep, with removable snap-top lids, approximately one-third filled with defaunated local sand.

Divers deployed six of each type of trap in adjacent groups just after dusk and retrieved them just after dawn on two successive nights in March 1985. Reentry traps were closed and trap bottles from emergence traps capped by divers before return to the surface. The moon was nearly new and rose late each night, thus providing little illumination. The first night's collections were made for 12.75 hours at a depth of 7 m and the second night's for 11.5 hours at a depth of 20 m.

Animals in the collection bottles of the emergence traps were concentrated on a 95 μm mesh sieve, washed into sample bottles, and fixed in a buffered formalin-Rose Bengal solution (ca. 5% formalin final strength). Animals that had entered the reentry traps were washed from the sand with fresh water, causing them to release their grasp on sand grains (R. Higgins[1]). The contents of each trap were washed at least 5 times, and until no further animals could be seen in the wash water. All washings were sieved through a 95 μm mesh sieve. The retained material was then poured into sample bottles and fixed as above.

The stained, fixed animals in each sample were examined, identified, and counted with a stereomicroscope. Identifications were made to genus and

[1]R. Higgins, Smithsonian Institution, Washington, DC 20560.

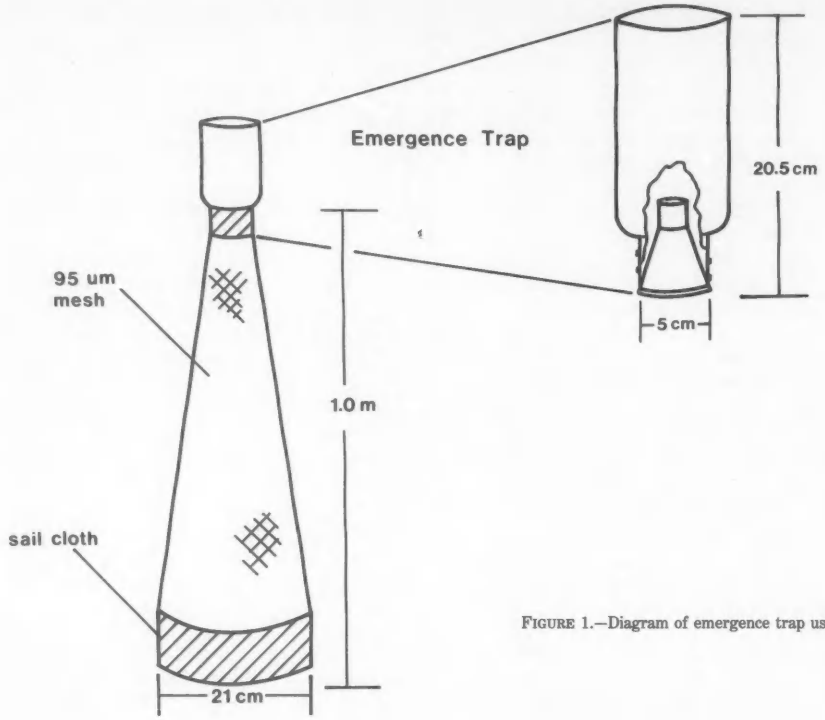

FIGURE 1.—Diagram of emergence trap used in this study.

species when possible; numbers of major taxa and groups are presented here for simplicity and comparative purposes.

Results

The zooplankton caught in the traps at Alligator Reef were dominated by copepods. Other taxa and categories that were collected included chaetognaths, nematodes, ostracods, polychaetes, cumaceans, isopods, amphipods, and mysids, as well as numerous others that were less common or frequently caught (Table 1). Many of these groups, such as the harpacticoid copepods, are well known as benthic or near-bottom forms. Others, such as the calanoid copepods, are known as primarily planktonic animals that are sometimes observed close to the bottom or other substrate. Many larval forms of benthic macroinvertebrates were captured, especially settling stages, such as barnacle cyprids and megalopae.

Comparisons of the total mean numbers of animals caught by each trap type and at each location show that approximately 4 times as many animals were caught by reentry traps as by emergence traps and that about twice as many animals were captured at the 7 m site as at the 20 m site (Table 1). Twelve common groups together accounted for 97.9% of all the animals caught. The results of two-way ANOVAs showed that reentry traps captured significantly more harpacticoid and cyclopoid copepods, ostracods, mysids, polychaetes, and nematodes than emergence traps, while the emergence traps captured significantly more calanoid copepods and isopods (Table 2). Significantly more cumaceans, gammarid amphipods, polychaetes, and nematodes were captured at the 20 m site than at the 7 m site, while significantly more calanoid copepods and chaetognaths were captured at the shallower location (Table 2). The two-way ANOVAs showed significant interaction effects between the trap types and sampling locations on the numbers of harpacticoid and

TABLE 1.—Demersal zooplankton captured in reentry and emergence traps at sand bottom sites (7 m and 20 m) near Alligator Reef, Florida in March 1985. Data are mean numbers of animals m^{-2} (SE).

	Emergence		Reentry	
Group	7 m	20 m	7 m	20 m
Harpacticoids[1]	754 (188)	3,040 (726)	16,108 (2,289)	8,866 (845)
Cyclopoids[1]	2,039 (508)	740 (165)	5,943 (1,071)	3,713 (478)
Nematodes[1]	11 (11)	13 (9)	8,840 (1,241)	823 (121)
Calanoids[1]	2,023 (421)	359 (128)	231 (80)	574 (209)
Copepod nauplii[1]	830 (248)	338 (99)	130 (53)	515 (121)
Ostracods[1]	51 (14)	35 (15)	498 (93)	360 (80)
Chaetognaths[1]	289 (47)	17 (8)	357 (70)	126 (65)
Halacarids	4 (4)	0	538 (160	0
Polychaetes[1]	29 (27)	69 (42)	94 (39)	314 (56)
Caprellid amphipods	0	117 (38)	4 (4)	170 (18)
Gammarid amphipods[1]	11 (5)	100 (49)	54 (19)	119 (32)
Cumaceans[1]	14 (5)	74 (51)	58 (23)	101 (18)
Mysids[1]	7 (5)	39 (8)	72 (27)	43 (18)
Larvaceans	112 (87)	0	29 (29)	11 (11)
Isopods[1]	62 (15)	35 (11)	7 (7)	33 (9)
Lancelets	0	0	14 (7)	69 (9)
Pycnogonids	4 (4)	39 (34)	0	0
Tanaids	0	36 (11)	0	0
Cyphonautes	0	0	0	29 (13)
Penaeids	0	9 (5)	0	18 (7)
Chiton larvae	0	0	11 (7)	7 (5)
Pagurid crabs	0	4 (4)	7 (5)	4 (4)
Cyprids	0	0	11 (7)	0
Hippid crabs	0	0	0	7 (5)
Magelona polychaetes	0	4 (4)	0	0
Fish larvae	0	4 (4)	0	0
Brachyuran crabs	0	4 (4)	0	0
Totals	6,240	5,076	33,006	15,902
Trap totals	11,316		48,908	
Site totals: 7 m: 39,250				
20 m: 20,978				
Grand total 60,228				

[1]"common" groups caught by both traps at both sites.

TABLE 2.—Results of 2-way ANOVAs comparing effects of sampling location and trap type on numbers of animals caught from 12 common groups. Data are mean/m^2 and F value for associated comparisons for each category; significantly higher means are underlined. For all comparisons df = 1, 19.

	Location			Trap			Interaction
Group	7 m	20 m	F	Emergence	Reentry	F	F
Harpacticoids	8,431	6,218	2.81	1,793	12,487	65.57**	14.33**
Cyclopoids	3,991	2,361	4.14	1,449	4,828	17.83**	1.17
Nematodes	4,426	454	36.80**	12	4,842	54.20**	41.70**
Calanoids	1,127	476	6.45**	1,267	402	11.39**	14.53**
Copepod nauplii	480	427	3.12	606	305	3.33	4.00
Ostracods	274	207	1.00	43	424	36.30**	1.75
Chaetognaths	323	77	19.51**	165	242	1.88	1.00
Polychaetes	61	203	12.07**	47	204	14.82**	3.69
Gammarid amphipods	32	110	7.26*	51	87	1.00	1.00
Cumaceans	36	89	4.41*	41	79	2.32	2.97
Mysids	40	41	1.00	22	58	4.92*	3.45
Isopods	34	33	1.00	49	20	6.94*	5.41*

* = $P < 0.05$, ** = $P < 0.01$.

calanoid copepods, isopods, and nematodes caught (Table 2), indicating that the capture rates of the two trap types varied between locations. Differences in the types and numbers of animals caught by each trap are more important, however.

Reentry traps were much more effective than emergence traps at capturing a greater variety of animals. The most striking differences are the much larger numbers of harpacticoid and cyclopoid copepods captured in reentry traps. In addition to quantitative differences the reentry traps also caught individuals of six groups that were not found in the emergence traps (Table 1). The six groups included the lancelets and five types of demersal larvae.

Conversely, emergence traps were more effective at capturing calanoid copepods and isopods. Specimens of five other taxa were captured only in emergence traps (Table 1).

Analysis of the capture rate of each common group by the two trap types shows significantly different assemblages ($\chi^2 = 881068$, df = 11, $P << 0.001$) (Fig. 2a). Furthermore, each trap type caught some relatively rare groups, meaning that the lower capture rate of the emergence traps did not prevent them from capturing groups that did not appear in the reentry traps. Analysis of the capture frequencies of these rarer groups shows that the two trap types capture different assemblages of organisms ($\chi^2 = 25806$, df = 9, $P << 0.001$) (Fig. 2b). Therefore, the reentry and emergence traps sampled different fauna or sampled the same fauna differently.

Discussion

Varying migration patterns and swimming behaviors by the various taxa and groups can explain the differences between the assemblages caught by the two trap types. Ascending animals would have to move 1 m off the bottom in order to be captured by the emergence traps. Descending animals would not have been captured at all by the emergence traps, but would only have needed to be a few cm off the bottom to enter the reentry traps. Thus, reentry traps are more likely to capture demersal organisms during their migration than emergence traps if many of these organisms never move very far up into the water column, as Alldredge and King (1985) have shown. Reentry traps also captured settling larvae, which presumably are migrating in only one direction prior to establishing a sessile mode of life. Such larval forms were a small fraction of the total numbers of animals caught, but could be a significant portion of the reentering fauna at times. Both trap types may have also captured some animals that are holoplanktonic as noted by Robichaux et al. (1981), despite our efforts to prevent this during deployment and recovery of the traps. Some animals may have entered the traps by crawling rather than from the plankton, as Scheibel (1974) observed. Finally, placement of the traps after dusk may have missed animals migrating at or before dusk, but the errors caused by this artifact, as well as errors due to incomplete recovery of animals, are not likely to alter our results significantly.

Another possible explanation for at least some of the differences between capture rates of the two trap types is differential avoidance of one trap type, in this case the emergence traps. Given that emergence traps consist of materials quite unlike those that demersal zooplankton would normally encounter it should not be surprising that they might seek to avoid contact with them. The narrow funnel placed in the mouth of the collection bottles, while necessary to retain animals that have entered the bottle, may exclude others altogether. Some demersal zooplankton, such as calanoid copepods, are well known to exhibit an escape response when placed in contact with surfaces. Reentry traps, on the other hand, work partly by replicating natural sand substrate, reducing the potential for avoidance.

The results show clearly that different sampling techniques yield variable numbers of animals, even within the same taxon, and collect different groups of animals. Thus, evaluation of the demersal zooplankton depends strongly on sampling techniques. Adoption of a single standard sampling technique might appear to be a resolution of the problem, but a standard approach should sample all the organisms that exhibit demersal behavior in a given area, and neither emergence trapping nor reentry traping does. Furthermore, Stretch (1985) has observed that not all members of a demersal population migrate each night, so trapping techniques that depend on animal migration must consistently underestimate the actual abundance of demersal organisms in association with a given substrate. Tendency to migrate may vary among species, within the life cycle of a given species and from day to day, making accurate sampling of the demersal zooplankton by trapping a logistical impossibility. Collection techniques that directly sample demersal organisms in or on the substrate, such as airlift sampling (Stretch 1985) or sediment coring techniques commonly used to sample meiofauna, should give more accurate abundance estimates, but must be used in conjunction with one or more trapping

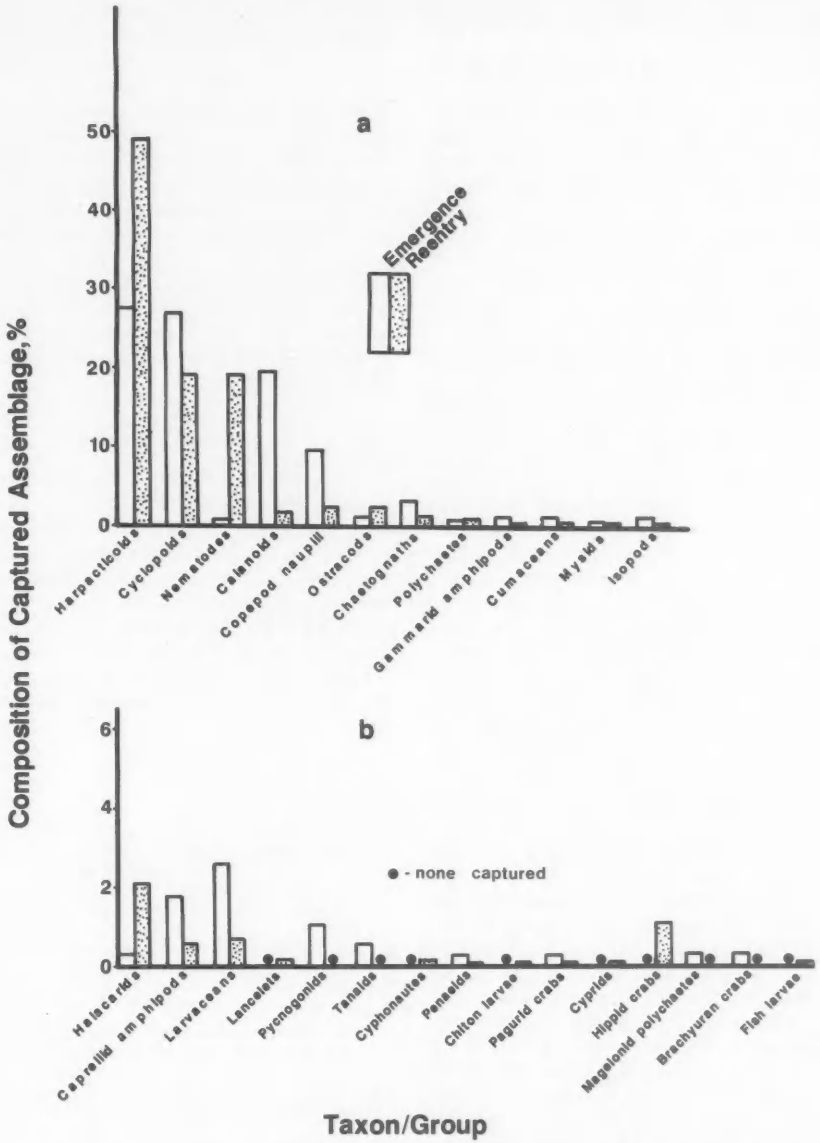

FIGURE 2.—Percentage of the total animals caught by each trap type by taxon or group, in rank order of total abundance, pooled over sites; a) common groups, b) rare groups.

techniques to distinguish migratory from nonmigratory populations.

Comparisons of demersal zooplankton abundances among studies are also made difficult by variation among the trap types and approaches used. Alldredge and King (1980) compared reentry and emergence traps, showing as we have that reentry traps captured very much larger numbers and different proportions of demersal organisms. Aside from studies by Stretch (1985) and ourselves (unpubl. data), we are unaware of any effort to use a direct sampling technique to calibrate a trapping technique. Thus, published abundance estimates for demersal zooplankton abundance are probably low and biased, reflecting the preponderant use of emergence trapping.

Robichaux et al. (1981) pointed out that animals entering traps by crawling can be a significant artifact. Such contamination would probably be a greater problem for reentry traps than for emergence traps. Our reentry traps captured large numbers of nematodes and harpacticoid copepods, which can enter by crawling, but even when they are eliminated altogether from the trap totals, reentry traps still caught twice as many animals as emergence traps (Table 1). Furthermore, at least some nematodes and harpacticoids do swim freely, even if they do not move very far up into the water column, as Alldredge and King (1985) have shown. Thus, we think that reentry trapping reliably yields higher estimates of demersal zooplankton abundance that are more realistic than results from emergence trapping but probably not truly accurate.

Robichaux et al. (1981) also argued that contamination of demersal zooplankton traps by holoplanktonic and crawling organisms causes an overestimate of the actual importance of demersal zooplankton in benthic food webs. We dispute this view on several grounds. First, the emergence trapping technique used by Robichaux et al. (1981), as is the case with others' use of emergence trapping, probably yielded significant underestimates of the actual abundance of demersal zooplankton, as we discuss above. Second, we suspect that all trapping techniques are likely to miss animals that are not migrating actively or that avoid traps, causing further population underestimates. Finally, estimates of demersal zooplankton populations resident within a given habitat may fail to reflect the actual availability of these animals as consumers or prey via transport.

Sand bottom habitats may be important sources of demersal zooplankton for consumers in other habitats. Currents can carry demersal organisms passively to other habitats. Animals that migrate high into the water column, such as the groups captured especially well by emergence traps, may be carried relatively great distances compared with those that crawl or stay within the near-bottom boundary layer. Furthermore, off-reef foraging by reef dwellers may allow exploitation of demersal organisms on sandy bottoms in the absence of advection. If so, estimates of demersal zooplankton abundance derived from reentry trapping will again be realistic, if not accurate, from the standpoint of community ecology. Therefore, demersal zooplankton are potentially quite important to marine benthic communities, even if the techniques used to sample them are imperfect.

Acknowledgments

This research was made possible with support provided by the NOAA-National Undersea Research Program at the University of North Carolina, (UNC), Wilmington, to Lawrence B. Cahoon and G. Simmons, who graciously shared shiptime. Support was also provided by UNC Sea Grant (R/MG 84-07 and R/MG 85-01), the National Science Foundation (RII 8311 486), the American Philosophical Society, the Lerner-Grey Fund for Marine Research and the North Carolina Collegiate Academy of Sciences.

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INDEX

Fishery Bulletin: Vol. 86, No. 1-4

ABLE, KENNETH W.—see GRIMES et al.

"Accumulation of age pigments (lipofuscin) in two cold-water fishes," by Maria Vernet, John R. Hunter, and Russell D. Vetter, 401

"Age and growth of larval gulf menhaden, *Brevoortia patronus*, in the northern Gulf of Mexico," by Stanley M. Warlen, 77

"Age, morphology, developmental biology, and biochemical genetic variation of Yukon River fall chum salmon, *Oncorhynchus keta*, and comparisons with British Columbia populations," by Terry D. Beacham, Clyde B. Murray, and Ruth E. Withler, 663

"Age-specific vulnerability of Pacific sardine, *Sardinops sagax*, larvae to predation by northern anchovy, *Engraulis mordax*," by John L. Butler and Darlene Pickett, 163

Ageing studies
  lipofuscin in larval fish, 401
  menhaden, gulf, 77
  see also Otoliths

Algae, benthic
  recruitment of spiny lobsters, 331

Allocyttus sp.—see Oreo, black

Alosa sapidissima—see Shad, American

Alvinocaris markensis
  new decapod crustacean species, 263

Alvinocaris muricola
  new decapod crustacean species, 263

Alvinocaris spp.
  key to species, 263

Alvinocaris stactophila
  new decapod crustacean species, 263

AL-YAMANI, J.—see DAGG et al.

Amphipods
  shrimp diets, 543

"Analyses of the relationship between the distribution of searching effort, tuna catches, and dolphin sightings within individual purse seine cruises," by Tom Polacheck, 351

Anchovy, northern
  predation on sardine larvae, 163

Anoplopoma fimbria—see Sablefish

"Appendage injury in Dungeness crabs, *Cancer magister*, in southeastern Alaska," by Susan M. Shirley and Thomas C. Shirley, 156

Apristurus brunneus—see Shark, scyliorhinid

Armorhead, pelagic
  biogeography, 453

ARMSTRONG, DAVID A.—see ROGERS et al.

ARNOLD, CONNIE R.—see BROWN-PETERSON et al.

"Aspects of the biology of two scyliorhinid sharks, *Apristurus brunneus* and *Parmaturus xaniurus*, from the upper continental slope off southern California," by Jeffrey N. Cross, 691

Atheresthes evermanni—see Flounder, kamchatka

Atheresthes stomias—see Flounder, arrowtooth

Atlantic croaker
  distribution and abundance, 129

BAGLIVO, JENNY A.—see BROUSSEAU and BAGLIVO

Banded drum
  distribution and abundance, 129

BARLOW, JAY, "Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: I. Ship surveys," 417

BARLOW, JAY, CHARLES W. OLIVER, TERRY D. JACKSON, and BARBARA L. TAYLOR, "Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: II. Aerial surveys," 433

BARSHAW, DIANA E., and DONALD R. BRYANT-RICH, "A long-term study on the behavior and survival of early juvenile American lobster, *Homarus americanus*, in three naturalistic substrates: eelgrass, mud, and rocks," 789

Bass, striped
  stomach contents, 397

BAYLIFF, WILLIAM H., "Integrity of schools of skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean, as determined from tagging data," 631

BEACHAM, TERRY D., CLYDE B. MURRAY, and RUTH E. WITHLER, "Age, morphology, developmental biology, and biochemical genetic variation of Yukon River fall chum salmon, *Oncorhynchus keta*, and comparisons with British Columbia populations," 663

BECKER, D. SCOTT, "Relationship between sediment character and sex segregation in English sole, *Parophrys vetulus*," 517

"Behavior of southern right whales, *Eubalaena australis*, feeding

feeding on the Antarctic krill, *Euphausia superba*," by William M. Hamner, Gregory S. Stone, and Bryan S. Obst, 143

Behavior studies
English sole, 830
lobster, American, 791
plankton, 842

Biochemical genetics—see Genetic studies

Black drum
distribution and abundance, 129
trotline fishery, 109

BLAYLOCK, ROBERT A., "Distribution and abundance of bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), in Virginia," 797

Bluefish
spawning season, 237

BOEHLERT, GEORGE W., and TAKASHI SASAKI, "Pelagic biogeography of the armorhead, *Pseudopentaceros wheeleri*, and recruitment to isolated seamounts in the North Pacific Ocean," 453

BOLZ, GEORGE R., and R. GREGORY LOUGH, "Growth through the first six months of Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, based on daily otolith increments," 223

Boonea impressa—see Snail, pyramidellid

Bootstrap method
sablefish abundance, 445

BOURKE, ROBERT E.—see WATSON et al.

Breeding habits—see Reproductive studies

Brevoortia patronus—see Menhaden, gulf

BRILL, RICHARD W.—see WATSON et al.

BROOKS, E. R.—see MULLIN and BROOKS

BROUSSEAU, DIANE J., and JENNY A. BAGLIVO, "Life tables for two field populations of soft-shell clam, *Mya arenaria*, (Mollusca: Pelecypoda) from Long Island Sound," 567

BROWN-PETERSON, NANCY, PETER THOMAS, and CONNIE R. ARNOLD, "Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in South Texas," 373

BRUCE, B. D., "Larval development of blue grenadier, *Macruronus novaezelandiae* (Hector), in Tasmanian waters," 119

BRYANT-RICH, DONALD R.—see BARSHAW and BRYANT-RICH

BUTLER, JOHN L.—see WATANABE et al.

BUTLER, JOHN L., and DARLENE PICKETT, "Age-specific vulnerability of Pacific sardine, *Sardinops sagax*, larvae to predation by northern anchovy, *Engraulis mordax*," 163

BUTLER, MARK J., IV—see HERRNKIND et al.

Bythograea mesatlantica
new decapod species, 263

CAHOON, LAWRENCE B., and CRAIG R. TRONZO, "A comparison of demersal zooplankton collected at Alligator Reef, Florida, using emergence and reentry traps," 838

CALLAHAN, MICHAEL W.—see SEKI and CALLAHAN

Cancer magister—see Crab, Dungeness

Cancer oregonensis—see Crab, *Cancer*

Carbon isotopes
shrimp diets, 543

Caridea: Bresilidae
key to species, 263

CASTRO, MARGARIDA, and KARIM ERZINI, "Comparison of two length-frequency based packages for estimating growth and mortality parameters using simulated samples with varying recruitment patterns," 645

Catsharks—see Shark, scyliorhinid

Chacellus filiformis
bathymetric and geographic distribution, 67

Char, Arctic
predation on salmon, 611

CHEN, CHE-TSUNG, TZYH-CHANG LEU, and SHOOU-JENG JOUNG, "Notes on reproduction in the scalloped hammerhead, *Sphyrna lewini*, in northeastern Taiwan waters," 389

CHESS, JAMES R.—see HOBSON and CHESS

Clam, soft-shell
life tables, 567

Cod, Atlantic
growth, 223

"Cojoined twin adult shrimp (Decapoda: Penaeidae)," by Austin B. Williams, 595

COLLINS, MARK R., and CHARLES A. WENNER, "Occurrence of young-of-the-year king, *Scomberomorus cavalla*, and Spanish, *S. maculatus*, mackerels in commercial-type shrimp trawls along the Atlantic coast of the southeast United States," 394

Cololabis saira—see Saury, Pacific

"A comparison of demersal zooplankton collected at Alligator Reef, Florida, using emergence and reentry traps," by Lawrence B. Cahoon and Craig R. Tronzo, 838

"Comparison of two length-frequency based packages for estimating growth and mortality parameters using simulated samples with varying recruitment patterns," by Margarida Castro and Karim Erzini, 645

"A comprehensive theory on the etiology of burnt tuna," by Cheryl Watson, Robert E. Bourke, and Richard W. Brill, 367

CONOVER, DAVID O.—see NYMAN and CONOVER

Copepod nauplii
distribution and abundance, 319

COSTON-CLEMENTS, LINDA—see HOSS et al.

COUTU, J.-M.—see DUTIL and COUTU

COWAN, JAMES H., JR., and RICHARD F. SHAW, "The distribution, abundance, and transport of larval sciaenids collected during winter and early spring from the continental shelf waters off west Louisiana," 129

Crab, *Cancer*
occurrence off British Columbia, 525

Crab, Dungeness
abundance, 603
appendage injury, 156
dissolved oxygen levels, 604
megalopae associations, 299

Crab, Gulf stone
megalopa stage, 289

CRANE, S. A.—see DAVIES et al.

Crassostrea gigas—see Oyster, Japanese

Crassostrea virginica—see Oyster, American

CRECCO, VICTOR A.—see SAVOY and CRECCO

Croaker, Atlantic
metabolic responses to temperatures, 483

Croaker, white
food-seeking, 251

CROSS, JEFFREY N., "Aspects of the biology of two scyliorhinid sharks, *Apristurus brunneus* and *Parmaturus xaniurus*, from the upper continental slope off southern California," 691

Crustacean, decapod
bathymetric and geographic distribution, 67

CURRENS, KENNETH P., CARL B. SCHRECK, and HIRAM M. LI, "Reexamination of the use of otolith nuclear dimensions to identify juvenile anadromous and nonanadromous rainbow trout, *Salmo gairdneri*," 160

Cynoscion arenarius—see Seatrout, sand

Cynoscion nebulosus—see Seatrout, spotted

Cynoscion regalis—see Weakfish

DAGG, M. J., P. B. ORTNER, and J. AL-YAMANI, "Winter-time distribution and abundance of copepod nauplii in the northern Gulf of Mexico," 319

DAVIES, N. M., R. W. GAULDIE, S. A. CRANE, and R. K. THOMPSON, "Otolith ultrastructure of smooth oreo, *Pseudocyttus maculatus*, and black oreo, *Allocyttus* sp., species," 499

DEW, C. BRAXTON, "Stomach contents of commercially caught Hudson River striped bass, *Morone saxatilis*, 1973–1975," 397

Diet—see Food habits

Disease studies
oysters, American, 553

Dissodactylus juveniles
bathymetric and geographic distribution, 67

Dissolved oxygen levels
prawn mortality, 601

"The distribution, abundance, and transport of larval sciaenids collected during winter and early spring from the continental shelf waters off west Louisiana," by James H. Cowan, Jr. and Richard F. Shaw, 129

"Distribution and abundance of bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), in Virginia," by Robert A. Blaylock, 797

DITTY, JAMES G., GLEN G. ZIESKE, and RICHARD F. SHAW, "Seasonality and depth distribution of larval fishes in the northern Gulf of Mexico above latitude 26°00′N," 811

DOERZBACHER, JEFF F.—see McEACHRON et al.

Dolly Varden
salmon predation, 613

Dolphin, bottlenose
population studies, 797

Dolphin, spotted
sightings within tuna, purse seine cruises, 351

DUTIL, J-D., and J.-M. Coutu, "Early marine life of Atlantic salmon, *Salmo salar*, postsmolts in the northern Gulf of St. Lawrence," 197

Early marine life of Atlantic salmon, *Salmo salar*, postsmolts in the northern Gulf of St. Lawrence," by J.-D. Dutil and J.-M. Coutu, 197

"An econometric analysis of net investment in Gulf shrimp fishing vessels," by John B. Penson, Jr., Ernest O. Tetty, and Wade L. Griffin, 151

Economic studies
fishery capital stock and investment approach, 339
shrimp fishing vessels, 151
tuna, "burnt", 367

"The effect of the ectoparasitic pyramidellid snail, *Boonea impressa*, on the growth and health of oysters, *Crassostrea virginica*, under field conditions," by Elizabeth A. Wilson, Eric N. Powell, and Sammy M. Ray, 553

"The effects of siltation on recruitment of spiny lobsters, *Panulirus argus*," by William F. Herrnkind, Mark J. Butler IV, and Richard A. Tankersley, 331

El Niño
ichthyoplankton off Chile, 1

"Electrophoretic identification of early juvenile yellowfin tuna, *Thunnus albacares*," by John E. Graves, Marie A. Simovich, and Kurt M. Schaefer, 835

ELSTON, RALPH A.—see FARLEY et al.

EMLEN, JOHN M.—see McINTYRE et al.

English sole
population studies, 826

Engraulis mordax—see Anchovy, northern

Environmental studies
ichthyoplankton off Chile, 1
rockfish, blue, 715
see also Feeding habitats; Habitat studies

Enzymes
tuna, "burnt", 367

EPIFANIO, CHARLES E., DAVID GOSHORN, and TIMOTHY E. TARGETT, "Induction of spawning in the weakfish, *Cynoscion regalis*," 168

ERZINI, KARIM—see CASTRO and ERZINI

"Estimation of natural mortality in fish stocks: A review," by E. F. Vetter, 25

Estuarine studies
shrimp, penaeid, 543

Eubalaena australis—see Whales, southern right

Euchirograpsus americanus
bathymetric and geographic distribution, 67

Euphausia superba—see Krill, Antarctic

"Evaluation of variability in sablefish, *Anoplopoma fimbria*, abundance indices in the Gulf of Alaska using the bootstrap method," by Michael F. Sigler and Jeffrey T. Fujioka, 445

"Experimental manipulation of population density and its effects on growth and mortality of juvenile western rock lobsters, *Panulirus cygnus* George," by Richard F. Ford, Bruce F. Phillips, and Lindsay M. Joll, 773

"Extractable lipofuscin in larval marine fish," by M. M. Mullin and E. R. Brooks, 407

FARLEY, C. AUSTIN, PETER H. WOLF, and RALPH A. ELSTON, "A long-term study of 'microcell' disease in oysters with a description of a new genus, *Mikrocytos* (g. n.), and two new species, *Mikrocytos mackini* (sp. n.) and *Mikrocytos roughleyi* (sp. n.)," 581

"The feeding habits of two deep slope snappers, *Pristipomoides zonatus* and *P. auricilla*, at Pathfinder Reef, Mariana Archipelago," by Michael P. Seki and Michael W. Callahan, 807

Feed habitats
mesotide areas, 703
see also Food habits

"A field method for determining prey preferences of predators," by N. B. Hargreaves, 763

FELDER, DARRYL L.—see MARTIN et al.

FINN, JAMES E.—see McINTYRE et al.

Fish habitats—see Habitat studies

FISHER, JOSEPH P.—see PEARCY and FISHER

Fishery, commercial
capital stock and investment approach, 339
flounder, yellowtail, 91
Hawaiian handline, 367
reducing bycatch using trotline, 109
tuna, 351, 367

Fishes
associations with crab megalopae, 299

Flatfish
population studies, 826

Flounder, arrowtooth
morphological comparison, 608

Flounder, gulf
growth studies, 832

Flounder, kamchatka
morphological comparison, 608

Flounder, yellowtail
variation in CPUE, 91

Food habits
bass, striped, 397
croaker, white, 251
rockfish, blue, 717
salmon, Pacific, 213
salmon postsmolts, 197
salmon predation, 613
shark, scyliorhinid, 697
shrimp, penaeid, 543
snapper, 807
whales, southern right, 143

"Food habits and daily ration of Greenland halibut, *Reinhardtius hippoglossoides*, in the eastern Bering Sea," by M. S. Yang and P. A. Livingston, 675

"Food pathways associated with penaeid shrimps in a mangrove-fringed estuary," by Allan W. Stoner and Roger J. Zimmerman, 543

FORD, RICHARD F., BRUCE F. PHILLIPS, and LINDSAY M. JOLL, "Experimental manipulation of population density and its effects on growth and mortality of juvenile western rock lobsters, *Panulirus cygnus* George," 773

FUJIOKA, JEFFREY T.—see SIGLER and FUJIOKA

"Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: A correction," by Peter H. Wiebe, 833

"Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish," by Alan L. Shanks, 703

Gadus morhua—see Cod, Atlantic

GAULDIE, R. W.—see DAVIES et al.

Gear, trawls
crab sampling, 529

Genetic studies
salmon, chum, 665

Genyonemus lineatus—see Croaker, white

Glycogen, muscle
spawning of sea scallop, 597

GOSHORN, DAVID—see EPIFANIO et al.

GOULD, EDITH, DIANE RUSANOWSKY, and DONNA A. LUEDKE, "Note on muscle glycogen as an indicator of spawning potential in the sea scallop, *Placopecten magellanicus*," 597

GRAVES, JOHN E., MARIE A. SIMOVICH, and KURT M. SCHAEFER, "Electrophoretic identification of early juvenile yellowfin tuna, *Thunnus albacares*," 835

GREEN, ALBERT W.—see McEACHRON et al.

Grenadier, blue
larval development, 119

GRIFFIN, WADE L.—see PENSON et al.

GRIMES, CHURCHILL B., CHARLES F. IDELBERGER, KENNETH W. ABLE, and STEPHEN C. TURNER, "The reproductive biology of tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, from the United States Mid-Atlantic Bight, and the effects of fishing on the breeding system," 745

"Growth of Pacific saury, *Cololabis saira*, in the northeastern and northwestern Pacific Ocean," by Yoshiro Watanabe, John L. Butler, and Tsukasa Mori, 489

Growth studies
cod, Atlantic, 223
flounder, gulf, 832
haddock, 223
lobster, American, 789
lobster, spiny, 775
menhaden, gulf, 77
saury, Pacific, 489
tropical fish, 645

"Growth through the first six months of Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, based on daily otolith increments," by George R. Bolz and R. Gregory Lough, 223

GUNDERSON, DONALD R.—see ROGERS et al.

Habitat studies
fishing efffects, 746
mesotide areas, 703
lobster, American, 791
rockfish, blue, 719

Haddock
growth, 223

Halibut, Greenland
food habits, 675

HAMNER, WILLIAM M., GREGORY S. STONE, and BRYAN S. OBST, "Behavior of southern right whales, *Eubalaena australis*, feeding on the Antarctic krill, *Euphausia superba*," 143

Haplosporidium nelsoni
parasitic effects on oysters, 553

"Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: I. Ship surveys," by Jay Barlow, 417

"Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: II. Aerial surveys," by Jay Barlow, Charles W. Oliver, Terry D. Jackson, and Barbara L. Taylor, 433

HARGREAVES, N. B., "A field method for determining prey preferences of predators," 763

Hatchery studies
salmon, coho, 173
smolt release, 655

Hedonic approach
fishery capital stock and investment, 339

HERRNKIND, WILLIAM F., MARK J. BUTLER IV, and RICHARD T. TANKERSLEY, "The effects of siltation on recruitment of spiny lobsters, *Panulirus argus*," 331

HOBSON, EDMUND S., and JAMES R. CHESS, "Trophic relations of the blue rockfish, *Sebastes mystinus*, in a coastal upwelling system off northern California," 715

Homarus americanus—see Lobster, American

HOSS, DONALD E., LINDA COSTON-CLEMENTS, DAVID S. PETERS, and PATRICIA A. TESTER, "Metabolic responses of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae to cold temperatures encountered following recruitment to estuaries," 483

Humboldt Current area
ichthyoplankton off Chile, 1

HUNTER, JOHN R.—see VERNET et al.

Hydrothermal discharge
Alvinocaris spp., 263

Ichthyoplankton—see Plankton studies

IDELBERGER, CHARLES F.—see GRIMES et al.

Identification methods
tuna, yellowfin, 835

"Induction of spawning in the weakfish, *Cynoscion regalis*," by Charles E. Epifanio, David Goshorn, and Timothy E. Targett, 168

"Integrity of schools of skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean, as determined from tagging data," by William H. Bayliff, 631

"Interannual variation of ichthyoplankton composition and abundance relations off northern Chile, 1964–85," by Valerie J. Loeb and Omar Rojas, 1

JAHN, A. E., D. M. GADOMSKI, and M. L. SOWBY, "On the role of food-seeking in the suprabenthic habit of larval white croaker, *Genyonemus lineatus* (Pisces: Sciaenidae)," 251

JAMIESON, GLEN S., and ANTAN C. PHILLIPS, "Occurrence of *Cancer* crab (*C. magister* and *C. oregonensis*) magalopae off the west coast of Vancouver Island, British Columbia," 525

JAMIESON, GLEN S., and ELLEN K. PIKITCH, "Vertical distribution and mass mortality of prawns, *Pandalus platyceros*, in Saanich Inlet, British Columbia," 601

JOLL, LINDSAY M.—see FORD et al.

JOUNG, SHOOU-JENG—see CHEN et al.

Kingfish, southern
distribution and abundance, 129

KIRKLEY, JAMES E., and DALE E. SQUIRES, "A limited information approach for determining capital stock and investment in a fishery," 339

KOSKI, K V.—see MURPHY et al.

Krill, Antarctic
feeding of whales, 143

Larimus fasciatus—see Banded drum

"Larval development of blue grenadier, *Macruronus novaezelandiae* (Hector), in Tasmanian waters," by B. D. Bruce, 119

Larval studies
cod, Atlantic, 223
continental shelf, 703
copepod nauplii, 319
crab, cancer, 525
crab, Dungeness, 299
crab, Gulf stone, 289
croaker, Atlantic, 483
croaker, white, 251
fishes, 299
grenadier, blue, 119
haddock, 223
ichthyoplankton off Chile, 1
lipofucin for ageing, 407
menhaden, gulf, 77
mesotide areas, 703
northern Gulf of Mexico, 811
sardine, Pacific, 163
sciaenids, 129
spot, 483

Laurencia spp.—see Algae, benthic

Leiostomus xanthurus—see Spot

"Length-weight relationships for gulf flounder, *Paralichthys albigutta*, from North Carolina," by Glen W. Safrit and Frank J. Schwartz, 832

LEU, TZYH-CHANG—see CHEN et al.

LI, HIRAM M.—see CURRENS et al.

Life history studies
clams, soft shell, 567
juvenile Pacific salmon, 213
shark, scyliorhinid, 691

"Life tables for two field populations of soft-shell clam, *Mya arenaria*, (Mollusca: Pelecypoda) from Long Island Sound," by Diane J. Brousseau and Jenny A. Baglivo, 567

"A limited information approach for determining capital stock and investment in a fishery," by James E. Kirkley and Dale E. Squires, 339

LIN, BIING-HWAN, and NANCY A. WILLIAMS, "Specifying a functional form for the influence of hatchery smolt release on adult salmon production," 655

Line transect methods
porpoise, harbor, 429

Lipofuscin
ageing methods, 401
larval marine fish, 407

Lithodes maja
bathymetric and geographic distribution, 67

LIVINGSTON, P. A.—see YANG and LIVINGSTON

Lobster, American
behavior and survival, 789

Lobster, spiny
population studies, 773
siltation and recruitment, 331

LOEB, VALERIE J., and OMAR ROJAS, "Interannual variation of ichthyoplankton composition and abundance relations off northern Chile, 1964–85," 1

"A long-term study of 'microcell' disease in oysters with a description of a new genus, Mikrocytos (g. n.), and two new species, *Mikrocytos mackini* (sp. n.) and *Mikrocytos roughleyi* (sp. n.)," by C. Austin Farley, Peter H. Wolf, and Ralph A. Elston, 581

"A long-term study on the behavior and survival of early juvenile American lobster, *Homarus americanus*, in three naturalistic substrates: eelgrass, mud, and rocks," by Diana E. Barshaw and Donald R. Bryant-Rich, 789

Lopholatilus chamaeleonticeps—see Tilefishes

LOUGH, R. GREGORY—see BOLZ and LOUGH

LUEDKE, DONNA A.—see GOULD et al.

Mackerel, king
occurrence of in shrimp trawls, 394

Mackerel, Spanish
occurrence of in shrimp trawls, 394

Macruronus novaezelandiae—see Grenadier, blue

MARTIN, JOEL W., FRANK M. TRUESDALE, and DARRYL L. FELDER, "The megalopa stage of the Gulf stone crab, *Menippe adina* Williams and Felder, 1986, with comparison of megalopae in the genus *Menippe*," 289

Mathematical methods
abundance survey, 448
chi-square tests, 634
CPUE for yellowtail flounder, 91
investment in shrimp fishing vessels, 151
length-frequency distribution, 645
mortality in fish stocks, 25
population estimates, 617
regression equations, 833
salmon survival, 655

MATLOCK, GARY C.—see McEACHRON et al.

MAYO, RALPH K.—see O'Brien and MAYO

McEACHRON, LAWRENCE W., JEFF F. DOERZBACHER, GARY C. MATLOCK, ALBERT W. GREEN, and GARY E. SAUL, "Reducing the bycatch in a commercial trotline fishery," 109

McINTYRE, JOHN D., REGINALD R. REISENBICHLER, JOHN M. EMLEN, RICHARD L. WILMOT, and JAMES E. FINN, "Predation of Karluk River sockeye salmon by coho salmon and char," 611

"The megalopa stage of the Gulf stone crab, *Menippe adina* Williams and Felder, 1986, with comparison of megalopae in the genus *Menippe*," by Joel W. Martin, Frank M. Truesdale, and Darryl L. Felder, 289

Melanogrammus aeglefinus—see Haddock

MENDELSSOHN, ROY, "Some problems in estimating population sizes from catch-at-age data," 617

Menhaden, gulf
age and growth, 77

Menippe adina—see Crab, Gulf stone

Menticirrhus americanus—see Kingfish, southern

"Metabolic responses of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae to cold temperatures encountered following recruitment to estuaries," by Donald E. Hoss, Linda Coston-Clements, David S. Peters, and Patricia A. Tester, 483

"Microcell" disease
oysters, 581

Micropogonias undulatus—see Croaker, Atlantic

Microstomus pacificus—see Sole, Dover

Migration studies
salmon, Atlantic, 197
salmon, coho, 173
salmon, Pacific, 213

"Migrations of coho salmon, *Oncorhynchus kisutch*, during their first summer in the ocean," by William G. Pearcy and Joseph P. Fisher, 173

Mikrocytos mackini
"microcell" disease in oysters, 581

Mikrocytos roughleyi
"microcell" disease in oysters, 581

Mobula japanica
key to species, 56

Mobula munkiana
key to species, 60

Mobula, spp.—see Rays, mobulid

Mobula tarapacana
key to species, 62

Mobula thurstoni
key to species, 49

Monte Carlo method
abundance survey method, 448

MORI, TSUKASA—see WATANABE et al.

Morone saxatilis—see Bass, striped

"Morphological differences between two congeneric species of pleuronectid flatfishes: Arrowtooth flounder, *Atheresthes stomias*, and Kamchatka flounder, *A. evermanni*," by Mei-Sun Yang, 608

Mortality
estimates, 671
length-frequency analysis, 645
lobster, spiny, 777
methods of fish stock estimation, 25

MULLIN, M. M., and E. R. BROOKS, "Extractable lipofuscin in larval marine fish," 407

Munida forceps
bathymetric and geographic distribution, 67

Munida longipes
bathymetric and geographic distribution, 67

Munidopsis alvisca
new decapod species, 263

Munids
abundance, 602
dissolved oxygen levels, 604

MURPHY, MICHAEL L., JOHN F. THEDINGA, and K V. KOSKI, "Size and diet of juvenile Pacific salmon during seaward migration through a small estuary in southeastern Alaska," 213

MURRAY, CLYDE B.—see BEACHAM et al.

Mya arenaria—see Clam, soft-shell

"Natural history of the rays on the genus *Mobula* in the Gulf of California," by Guiseppe Notarbartolo-di-Sciara, 45

"New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine, and hydrocarbon seepage," by Austin B. Williams, 263

NOTARBARTOLO-DI-SCIARA, GUISEPPE, "Natural history of the rays on the genus *Mobula* in the Gulf of California," 45

"Note on muscle glycogen as an indicator of spawning potential in the sea scallop, *Placopecten magellanicus*," by Edith Gould, Diane Rusanowsky, and Donna A. Luedke, 597

"Notes on decapod and euphausiid crustaceans, continental margin, western Atlantic, Georges Bank to western Florida, USA," by Austin B. Williams, 67

"Notes on reproduction in the scalloped hammerhead, *Sphyrna lewini*, in northeastern Taiwan waters," by Che-Tsung Chen, Tzyh-Chang Leu, and Shoou-Jeng Joung, 389

NYMAN, ROBERT M., AND DAVID O. CONOVER, "The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York," 237

O'BRIEN, LORETTA, and RALPH K. MAYO, "Source of variation in catch per unit effort of yellowtail flounder, *Limanda ferruginea* (Storer), harvested off the coast of New England," 91

OBST, BRYAN S.—see HAMNER et al.

"Occurrence of young-of-the-year king, *Scomberomorus cavalla*, and Spanish, *S. maculatus*, mackerels in commercial-type shrimp trawls along the Atlantic coast of the southeast United States," by Mark R. Collins and Charles A. Wenner, 394

"Occurrence of *Cancer* crab (*C. magister* and *C. oregonensis*) megalopae off the west coast of Vancouver Island, British Columbia," by Glen S. Jamieson and Antan C. Phillips, 525

"Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon," by Jonathan M. Shenker, 299

"On the role of food-seeking in the suprabenthic habit of larval white croaker, *Genyonemus lineatus* (Pisces: Sciaenidae)," by A. E. Jahn, D. M. Gadomski, and M. L. Sowby, 251

Onchorhynchus gorbuscha—see Salmon, pink

Oncorhynchus keta—see Salmon, chum

Oncorhynchus kisutch—see Salmon, coho

Oncorhynchus nerka—see Salmon, sockeye

Oncorhynchus spp.—see Salmon, Pacific

Oreo, black
otolith ultrastructure, 499

Oreo, smooth
otolith ultrastructure, 499

ORTNER, P. B.—see DAGG et al.

Ostrea edulis—see Oyster, flat

Ostrea lusida—see Oyster, Olympia

"Otolith ultrastructure of smooth oreo, *Pseudocyttus maculatus*, and black oreo, *Allocyttus* sp., species," by N. M. Davies, R. W. Gauldie, S. A. Crane, and R. K, Thompson, 499

Otoliths
bluefish, 237
cod, Atlantic, 223
haddock, 223
menhaden, gulf, 77
oreo, black, 499
oreo, smooth, 499
saury, Pacific, 489
trout, rainbow, 160

Oyster, American
growth and health, 553

Oyster, flat
"microcell" disease, 581

Oyster, Japanese
"microcell" disease, 581

Oyster, Olympia
"microcell" disease, 581

Pandalus jordani—see Shrimp, pink

Pandalus platyceros—see Prawn, spot

Panulirus argus—see Lobster, spiny

Panulirus cygnus—see Lobster, spiny

Parasite studies
oyster growth, 553
oysters, 581

Parmaturus xaniurus—see Shark, scyliorhinid

Parophrys vetulus—see English sole

Pathology
oysters, 581

PEARCY, WILLIAM G., and JOSEPH P. FISHER, "Migrations of coho salmon, *Oncorhynchus kisutch*, during their first summer in the ocean," 173

"Pelagic biogeography of the armorhead, *Pseudopentaceros wheeleri*, and recruitment to isolated seamounts in the North Pacific Ocean," by George W. Boehlert and Takashi Sasaki, 453

Penaeus brasiliensis—see Shrimps, penaeid

Penaeus notialis—see Shrimps, penaeid

Penaeus subtilis—see Shrimps, penaeid

PENSON, JOHN B., JR., ERNEST O. TETTY, and WADE L. GRIFFIN, "An econometric analysis of net investment in Gulf shrimp fishing vessels," 151

Perkinsus marinus
parasitic effects on oysters, 553

PETERS, DAVID S.—see HOSS et al.

PHILLIPS, ANTAN C.—see JAMIESON and PHILLIPS

PHILLIPS, BRUCE F.—see FORD et al.

Phocoena phocoena—see Porpoise, harbor

PICKETT, DARLENE—see BUTLER and PICKETT

PIKITCH, ELLEN K.—see JAMIESON and PIKITCH

Placopecten magellanicus—see Scallop, sea

Plankton studies, 1, 129, 299, 704, 723, 811, 833, 838

Pogonias cromis—see Black drum

POLACHECK, TOM, "Analyses of the relationship between the distribution of searching effort, tuna catches, and dolphin sightings within individual purse seine cruises," 351

Polychaetes, capitellid
shrimp diets, 543

Pomatomus saltatrix—see Bluefish

Population studies
dolphin, bottlenose, 797
English sole, 823
larval fishes, 811
lobster, spiny, 775
mackerel, Pacific, 622
methods, 617
porpoise, harbor, 417, 433
sablefish, 445
salmon, chum, 663
shark, scyliorhinid, 694

Porpoise, harbor
abundance estimation, 417, 433

Postsmolts
salmon, Atlantic, 197

POWELL, ERIC N.—see WILSON et al.

Prawn, spot
distribution and mortality, 601

Predation
salmon, 763
sardine larvae, 163

"Predation of Karluk River sockeye salmon by coho salmon and char," by John D. McIntyre, Reginald R. Reisenbichler, John M. Emlen, Richard L. Wilmot, and James E. Finn, 611

Pristipomoides auricilla—see Snapper

Pristipomoides zonatus—see Snapper

Pseudocyttus maculatus—see Oreo, smooth

Pseudopentaceros wheeleri—see Armorhead, pelagic

Purse seine
salmon, coho, 173
searching effort, tuna catches, and dolphin sightings, 351

RAY, SAMMY M.—see WILSON et al.

Rays, mobulid
natural history, 45
key to species, 48

Red drum
reducing bycatch, 109

"Reducing the bycatch in a commercial trotline fishery," by Lawrence W. McEachron, Jeff F. Doerzbacher, Gary C. Matlock, Albert W. Green, and Gary E. Saul, 109

"Reexamination of the use of otolith nuclear dimensions to identify juvenile anadromous and nonanadromous rainbow trout, *Salmo gairdneri*," by Kenneth P. Currens, Carl B. Schreck, and Hiram M. Li, 160

Reinhardtius hippoglossoides—see Halibut, Greenland

REISENBICHLER, REGINALD R.—see McINTYRE et al.

"The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York," by Robert M. Nyman and David O. Conover, 237

"Relationship between sediment character and sex segregation in English sole, *Parophrys vetulus*," by D. Scott Becker, 517

"Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in South Texas," by Nancy Brown-Peterson, Peter Thomas, and Connie R. Arnold, 373

"The reproductive biology of tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, from the United States Mid-Atlantic Bight, and the effects of fishing on the breeding system," by Churchill B. Grimes, Charles F. Idelberger, Kenneth W. Able, and Stephen C. Turner, 745

Reproductive studies
bluefish, 237
larval fishes, 811
oyster, American, 553
scallop, sea, 597
seatrout spawning, 129
seatrout, spotted, 373
shark, hammerhead, 389
tilefishes, 745, 752
weakfish, 168

Rockfish, blue
habitat studies, 715

ROGERS, CHRISTOPHER W., DONALD R. GUNDERSON, and DAVID A. ARMSTRONG, "Utilization of a Washington estuary by juvenile English sole, *Parophrys vetulus*," 823

ROJAS, OMAR—see LOEB and ROJAS

RUSANOWSKY, DIANE—see GOULD et al.

Sablefish
abundance indices, 445

Saccostrea commercialis—see Oyster, flat

SAFRIT, GLEN W., and FRANK J. SCHWARTZ, "Length-weight relationships for gulf flounder, *Paralichthys albigutta*, from North Carolina," 832

Salmo gairdneri—see Trout, rainbow

Salmo salar—see Salmon, Atlantic

Salmon, Atlantic
postsmolts, 197

Salmon, chum
population spawning, 663
size and diet of juveniles, 213
smolts and adult production, 655

Salmon, coho
ocean migrations, 173
predation, 611
predators, 763
size and diet of juveniles, 213
smolts and adult production, 655

Salmon, Pacific
size and diet of juveniles, 213

Salmon, pink
predators, 763
size and diet of juveniles, 213

Salmon, sockeye
predation, 611

Salvelinus alpinus—see Char, Arctic

Salvelinus malma—see Dolly Varden

Sampling techniques
plankton, 838
sole, English, 517

Sardine, Pacific
vulnerability to predation, 163

Sardinops sagax—see Sardine, Pacific

SASAKI, TAKASHI—see BOEHLERT and SASAKI

SAUL, GARY E.—see McEACHRON et al.

Saury, Pacific
growth, 489

SAVOY, THOMAS F., and VICTOR A. CRECCO, "The timing and significance of density-dependent and density-independent mortality of American shad, *Alosa sapidissima*," 467

Scallop, sea
spawning potential, 597

SCHAEFER, KURT M.—see GRAVES et al.

Schooling
tuna, skipjack, 631

SCHRECK, CARL B.—see CURRENS et al.

Sciaenops ocellatus—see Red drum

Scomberomorus cavalla—see Mackerel, king

Scomberomorus maculatus—see Mackerel, Spanish

"Seasonality and depth distribution of larval fishes in the northern Gulf of Mexico above latitude 26°00'N," by James G. Ditty, Glen G. Zieske, and Richard F. Shaw, 811

Seatrout, sand
larval spawning, 129

Seatrout, spotted, 109
reproductive biology, 373

Sebastes mystinus—see Rockfish, blue

Sediment character
sex segregation in English sole, 517

SEKI, MICHAEL P., and MICHAEL W. CALLAHAN, "The feeding habits of two deep slope snappers, *Pristipomoides zonatus* and *P. auricilla*, at Pathfinder Reef, Mariana Archipelago," 807

Sex segregation
sole, English, 517

Shad, American
mortality rates, 467

SHANKS, ALAN L., "Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish," 703

Shark, scyliorhinid
biology, 691

Sharks, hammerhead
reproduction, 389

SHAW, RICHARD F.—see DITTY et al.

SHAW, RICHARD F.—see COWAN AND SHAW

SHENKER, JONATHAN M., "Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon," 299

SHIRLEY, SUSAN M., and THOMAS C. SHIRLEY, "Appendage injury in Dungeness crabs, *Cancer magister*, in southeastern Alaska," 156

SHIRLEY, THOMAS C.—see SHIRLEY and SHIRLEY

Shrimp, gulf
investment in fishing vessels, 151

Shrimp, pink
abundance, 603
dissolved oxygen levels, 604

Shrimp, roughback
cojoined (two headed) specimen, 595

Shrimps, penaeid
food pathways, 543

SIGLER, MICHAEL F., and JEFFREY T. FUJIOKA, "Evaluation of variability in sablefish, *Anoplopoma fimbria*, abundance indices in the Gulf of Alaska using the bootstrap method," 445

SIMOVICH, MARIE A.—see GRAVES et al.

"Size and diet of juvenile Pacific salmon during seaward migration through a small estuary in southeastern Alaska," by Michael L. Murphy, John F. Thedinga, and K V. Koski, 213

Snail, pyramidellid
parasitic effects on oysters, 553

Snapper
food habits, 807

Sole, Dover
lipofuscin for ageing, 401

Sole, English
sex segregation, 517

"Some problems in estimating population sizes from catch-at-age data," by Roy Mendelssohn, 617

"Sources of variation in catch per unit effort of yellowtail flounder, *Limanda ferruginea* (Storer), harvested off the coast of New England," by Loretta O'Brien and Ralph K. Mayo, 91

Spawning season
bluefish, 237

Spawning studies—see Reproductive studies

"Specifying a functional form for the influence of hatchery smolt release on adult salmon production," by Biing-Hwan Lin and Nancy A. Williams, 655

Sphyrna lewini—see Sharks, hammerhead

Sphyrna mokarran—see Sharks, hammerhead

Sphyrna zygaena—see Sharks, hammerhead

Spot
distribution and abundance, 129
metabolic responses to temperatures, 483

SQUIRES, DALE E.—see KIRKLEY and SQUIRES

Stenella attenuata—see Dolphin, spotted

Stomach contents
halibut, Greenland, 676

"Stomach contents of commercially caught Hudson River striped bass, *Morone saxatilis*, 1973–1975," by C. Braxton Dew, 397

STONE, GREGORY S.—see HAMNER et al.

STONER, ALLAN W., and ROGER J. ZIMMERMAN, "Food pathways associated with penaeid shrimps in a mangrove-fringed estuary," 543

Submersibles
decapod crustaceans, 67
prawn distribution, 602

Survey, Pacific
growth, 489

Surveys
aerial, 433
bootstrap, 445
ichthyoplankton off Chile, 1
lobster, spiny, 331
porpoise, harbor, 417
ship, 417
sole, English, 517

Tagging studies
tuna, skipjack, 631

TANKERSLEY, RICHARD T.—see HERRNKIND et al.

TARGETT, TIMOTHY E.—see EPIFANIO et al.

Temperature studies
spot, 483
croaker, Atlantic, 483

TESTER, PATRICIA A.—see HOSS et al.

TETTY, ERNEST O.—see PENSON et al.

THEDINGA, JOHN F.—see MURPHY et al.

THOMAS, PETER—see BROWN-PETERSON et al.

THOMPSON, R. K.—see DAVIES et al.

Thunnus albacares—see Tuna, yellowfin

Thunnus obesus—see Tuna, bigeye

Tide studies, 703

Tilefishes
reproductive biology, 745

"The timing and significance of density-dependent and density-independent mortality of American shad, *Alosa sapidissima*," by Thomas F. Savoy and Victor A. Crecco, 467

Trachypenaeus similis—see Shrimp, roughback

Trawls, shrimp
occurrence of mackerel, 394

TRONZO, CRAIG R.—see CAHOON and TRONZO

"Trophic relations of the blue rockfish, *Sebastes mystinus*, in a coastal upwelling system off northern California," by Edmund S. Hobson and James R. Chess, 715

Trotlines, 109

Trout, rainbow
lipofuscin for ageing, 401
otolith identification, 160

TRUESDALE, FRANK M.—see MARTIN et al.

Tuna
distribution within purse seine cruises, 351

Tuna, bigeye
burnt tuna 367

Tuna, "burnt"
etiology, 367

Tuna, skipjack
schooling, 631
tag studies, 631

Tuna, yellowfin
burnt tuna, 367
identification of juveniles, 835

Turbot—see Halibut, Greenland

TURNER, STEPHEN C.—see GRIMES et al.

Tursiops truncatus—see Dolphin, bottlenose

Upwelling and downwelling
northern California coast, 715
South Atlantic Bight, 703

"Utilization of a Washington estuary by juvenile English sole, *Parophrys vetulus*," by Christopher W. Rogers, Donald R. Gunderson, and David A. Armstrong, 823

VERNET, MARIA, JOHN R. HUNTER, and RUSSELL D. VETTER, "Accumulation of age pigments (lipofuscin) in two cold-water fishes," 401

"Vertical distribution and mass mortality of prawns, *Pandalus platyceros*, in Saanich Inlet, British Columbia," by Glen S. Jamieson and Ellen K. Pikitch, 601

VETTER, E. F., "Estimation of natural mortality in fish stocks: a review," 25

VETTER, RUSSELL D.—see VERNET et al.

WARLEN, STANLEY M., "Age and growth of larval gulf menhaden, *Brevoortia patronus*, in the northern Gulf of Mexico," 77

WATANABE, YOSHIRO, JOHN L. BUTLER, and TSUKASA MORI, "Growth of Pacific saury, *Cololabis saira*, in the northeastern and northwestern Pacific Ocean," 489

WATSON, CHERYL, ROBERT E. BOURKE, and RICHARD W., BRILL, "A comprehensive theory on the etiology of burnt tuna," 367

Wave slicks, 703

Weakfish
induction of spawning, 168

WENNER, CHARLES A.—see COLLINS and WENNER

Western rock lobster—see Lobster, spiny

Whales, southern right
behavior, 143
feeding, 143

WIEBE, PETER H., "Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: a correction," 833

WILLIAMS, AUSTIN B., "Cojoined twin adult shrimp (Decapoda: Penaeidae)," 595

WILLIAMS, AUSTIN B., "New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine, and hydrocarbon seepage," 263

WILLIAMS, AUSTIN B., "Notes on decapod and euphausiid crustaceans, continental margin, western Atlantic, Georges Bank to western Florida, USA," 67

WILLIAMS, NANCY A.—see LIN and WILLIAMS

WILMOT, RICHARD L.—see McINTYRE et al.

WILSON, ELIZABETH A., ERIC N. POWELL, and SAMMY M. RAY, "The effect of the ectoparasitic pyramidellid snail, *Boonea*

impressa, on the growth and health of oysters, *Crassostrea virginica*, under field conditions," 553

"Winter-time distribution and abundance of copepod nauplii in the northern Gulf of Mexico," by M. J. Dagg, P. B. Ortner, and J. Al-Yamani, 319

WITHLER, RUTH E.—see BEACHAM et al.

WOLF, PETER H.—see FARLEY et al.

YANG, M. S., and P. A. LIVINGSTON, "Food habits and daily ration of Greenland halibut, *Reinhardtius hippoglossoides*, in the eastern Bering Sea," 675

YANG, MEI-SUN, "Morphological differences between two congeneric species of pleuronectid flatfishes: Arrowtooth flounder, *Atheresthes stomias*, and Kamchatka flounder, *A. evermanni*," 608

Yukon River salmon, 563

ZIESKE, GLEN G.—see DITTY et al.

ZIMMERMAN, ROGER J.—see STONER and ZIMMERMAN

Zooplankton—see Plankton studies

NOTICE

NOAA Technical Reports NMFS published during first 6 months of 1988.

63. Stock assessment of the Atlantic menhaden, *Brevortia tyrannus* fishery. By Douglas S. Vaughan and Joseph W. Smith. January 1988, iii + 18 p., 13 tables, 17 figs.
64. Illustrated key to penaeoid shrimps of commerce in the Americas. By Isabel Pérez Farfante. April 1988, iv + 32 p., 49 figs.
65. History of whaling in and near North Carolina. By Randall R. Reeves and Edward Michell. March 1988, iii + 28 p., 5 tables, 10 figs.
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ERRATA

Fishery Bulletin Vol. 86, No. 3

Hoss, Donald E., Linda Coston-Clements, David S. Peters, and Patricia A. Tester, "Metabolic responses of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae to cold temperatures encountered following recruitment to estuaries," pages 483–488.

Bottom of page 484 should read as follows:

FIGURE 1.—Representative water-temperatures, salinities, and developmental stages of larval spot from the spawning area to Beaufort Inlet, North Carolina. Drawings from Powell and Gordy (1980) and Lippson and Moran (1974).

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Fishery Bulletin	3 6 6 - 3 7 0	28 Sept. 1988
3. FREQUENCY OF ISSUE: Quarterly	3A. NO. OF ISSUES PUBLISHED ANNUALLY: 4	3B. ANNUAL SUBSCRIPTION PRICE: $16.00

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Scientific Publications Office, NMFS
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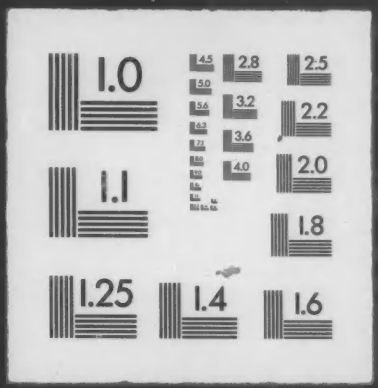
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